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Absolute Pitch: A (Re-)Examination of Electrophysiological Correlates

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Abstract

Absolute pitch (AP) is the rare and fascinating ability to recognize the pitch class of a tone without the aid of an external reference. Although many world-class composer and musicians have had AP, the ability seems to be relatively isolated from other musical and cognitive skills. As such, AP provides a unique window into how cognitive functions are developed and represented in the brain. However, the rarity of the phenomenon adversely affects the robustness of the neuroscientific research into it; most previous studies had to rely on small sample sizes. To reevaluate the neural basis of AP, the current doctoral thesis compares a large sample of musicians with and without AP.

The thesis comprises three research articles. Using electroencephalography (EEG), we measured the neural activity of the participating musicians during two experimental tasks and one task-free condition. In *article 1*, we repeated a previous experiment to investigate AP effects during passive listening. We successfully replicated the condition effects and null results of the original study but not the previously reported group difference between AP and non-AP musicians. In *article 2*, we examined functional connectivity during rest using two approaches. First, we attempted to replicate a previous finding of stronger connectivity between the left auditory cortex and the left dorsolateral prefrontal cortex in AP musicians. Second, we performed an exploratory whole-brain analysis. While our data provided no evidence for the importance of the previously reported connection, the whole-brain approach revealed networks with increased connectivity between auditory and frontal regions in the vicinity of the sylvian fissure. In *article 3*, we conducted an auditory Go/Nogo task to study how the presumed automaticity of AP affects the inhibitory load in AP musicians. Using two different Nogo conditions, we assessed the capability of both general auditory-related inhibition and specific suppression of pitch-labeling information. We found no evidence for group differences in behavioral or electrophysiological measures.

In summary, the findings of the thesis indicate that AP processes — and pitch labeling in particular — are not as automatically activated as is often assumed. Whether or not group

differences between AP and non-AP musicians can be observed in electrophysiological measures might depend on the specific task. The intrinsic functional brain networks additionally corroborate the importance of both early perceptual and later higher-cognitive processes in AP. Finally, our studies generally highlight the need for replications and large sample sizes in the field.

Zusammenfassung

Das absolute Gehör ist die seltene und faszinierende Fähigkeit, ohne die Zuhilfenahme eines Referenztons die Höhe eines Tons bestimmen zu können. Obwohl viele Komponisten und Musiker von Weltrang über das absolute Gehör verfügten, scheint es relativ unabhängig von anderen musikalischen und kognitiven Fähigkeiten zu sein. Dadurch bietet das absolute Gehör einen einzigartigen Einblick in die Entstehung und Repräsentation kognitiver Funktionen im Gehirn. Die Seltenheit des Phänomens beeinträchtigt allerdings dessen neurowissenschaftliche Erforschung, denn die meisten Studien beruhen auf kleinen Stichprobengrössen. In der vorliegenden Dissertation wird eine grosse Stichprobe von Musikern mit und ohne absolutes Gehör verglichen, um die neuronalen Grundlagen des absoluten Gehörs neu zu untersuchen und besser zu verstehen.

Die Dissertation umfasst drei Forschungsartikel. Mittels Elektroenzephalographie (EEG) haben wir die neuronale Aktivität der teilnehmenden Musiker während zweier experimenteller Aufgaben und im Ruhezustand gemessen. In *Artikel 1* wiederholten wir ein vorheriges Experiment, um Effekte des absoluten Gehörs während des passiven Zuhörens zu untersuchen. Wir konnten die Bedingungseffekte und Null-Ergebnisse der ursprünglichen Studie erfolgreich replizieren, nicht aber den zuvor berichteten Gruppenunterschied zwischen den zwei Musikergruppen. In *Artikel 2* untersuchten wir die funktionelle Konnektivität im Ruhezustand auf zwei Arten. Zum einen versuchten wir, den Befund einer anderen Studie zu replizieren. Dort waren der linke auditorische Cortex und der linke dorsolateralen präfrontalen Cortex (DLPFC) bei absolut hörenden Musikern stärker miteinander verbunden. Zum anderen führten wir eine explorative Analyse durch, bei der die Konnektivität im ganzen Gehirn berücksichtigt wurde. Unsere Daten konnten die Relevanz der Verbindung zwischen dem auditorischen Kortex und dem DLPFC nicht bekräftigen. Wir fanden aber andere Hinweise dafür, dass auditorische und frontale Hirnregionen entlang der Sylvischen Fissur bei Absoluthörenden stärker miteinander verbunden sind. In *Artikel 3* verwendeten wir ein auditorisches Go/Nogo-Paradigma, um zu untersuchen, wie sich die oft vermutete Automatizität des absoluten Gehörs auf

inhibitorische Prozesse auswirkt. Das Paradigma enthielt zwei verschiedenen Nogo-Bedingungen. Damit untersuchten wir einerseits allgemein die Fähigkeit zur Inhibition im auditorischen Bereich und andererseits spezifisch die Fähigkeit zur Inhibition der Tonhöhen-Benennung. Wir konnten weder in den behavioralen noch in den elektrophysiologischen Messwerten Gruppenunterschiede feststellen.

Die Befunde dieser Dissertation deuten darauf hin, dass die Prozesse, die dem absoluten Gehör unterliegen – insbesondere auch die Assoziation von Tönen mit Notennamen – nicht so automatisch sind, wie oft angenommen wird. Ob Gruppenunterschiede zwischen Musiker mit und ohne absolutes Gehör im EEG erkennbar sind, hängt möglicherweise vom spezifischen Aufgabenkontext ab. Die Ergebnisse der Netzwerkanalyse tragen ausserdem zur bisherigen Evidenz bei, dass sowohl frühe perzeptuelle als auch komplexere kognitive Prozesse eine Rolle spielen. Nicht zuletzt unterstreichen unsere Studien den allgemeinen Bedarf an Replikationen und grossen Stichprobengrössen in diesem Forschungsfeld.

Contents

Chapter 1 General Introduction

Absolute pitch (AP) — the ability to identify and/or produce a pitch without the aid of a reference tone (Deutsch, 2013) — is often associated with exceptional musical skills. Many renowned composers and performing musicians such as Mozart, Bach, Chopin, Beethoven, Heifetz, and Rubenstein are believed to have possessed AP (Deutsch, 2002; Sacks, 2007). The relative rarity of AP in Western cultures even among professional musicians only adds to the fascination of the phenomenon. Since its first scientific description in 1883 (Stumpf, 1883), AP has attracted ever-increasing interest not only from traditional music disciplines but also from other research areas including genetics and cognitive neuroscience (Deutsch, 2013). Because AP represents a highly specialized ability, unrelated to most other musical skills and cognitive functions (Levitin & Rogers, 2005; Zatorre, 2003), it may serve as model for understanding the interplay between genetic and environmental factors in the development and neural representation of cognitive functions (Zatorre, 2003). Furthermore, AP can provide insights into general aspects of perceptual processing, perceptual expertise, and pitch memory (Levitin & Rogers, 2005).

This thesis aims to (re-)evaluate the neural mechanisms underlying AP. Pitch identification in AP is fast and effortless (Deutsch, 2013), and thought to be highly automatic (Levitin & Rogers, 2005). Thus, differences between musicians with AP and musicians without AP might be detectable in the neurophysiological response to acoustic stimuli even if the musicians are not instructed to label the corresponding pitches. In AP musicians, the daily exposure to pitch-evoking sounds may further promote frequent co-activations of the brain regions involved in the pitch-labeling process. Due to their regularity, these co-activations might in turn be expressed in functional brain networks during rest (see Gabard-Durnam et al., 2016; Guerra-Carrillo et al., 2014). To examine such neurophysiological correlates of AP beyond deliberate pitch labeling, this thesis compares musicians with AP to musicians without AP both during acoustic stimulation and at rest by using electroencephalography (EEG).

The first part of the thesis gives a general overview of AP by introducing the concept of musical pitch, which is the basis for AP, and by reviewing the literature on the prevalence, the development, and the characteristics of AP (Chapter 1). The second part of the thesis focuses on the neural bases of AP and consists of three self-contained research articles on the electrophysiological correlates of AP (Chapter 2, Chapter 3, Chapter 4). The first research article (Chapter 2) addresses event-related potentials (ERPs) during a passive listening task with slight changes in pitch. The second research article (Chapter 3) examines functional connectivity networks during resting state. Both the first and the second research article include replication attempts of previous studies in a larger sample. The third research article reports an auditory Go/Nogo task requiring pitch-change detection but not pitch identification (Chapter 4). The final chapter of the thesis summarizes the empirical findings and discusses their implications (Chapter 5).

1.1 Pitch in Music

Musical tones can be described along three main perceptual dimensions: loudness, timbre, and pitch (Fletcher, 1934; Oxenham, 2013). Of these dimensions, pitch is particularly important to Western music. When arranged in a series and combined simultaneously, pitch gives rise to melodies and harmonies, both indispensable elements of most musical pieces (Oxenham, 2013; Plack et al., 2014). Pitch, loudness, and timbre are each closely related to physical properties of sound. Physically, all sounds arise from vibrations that propagate as sound pressure waves through a sound-transmitting medium. For musical tones, among many other sounds including speech, these sound pressure waves repeat periodically over time (Krumhansl, 2000; Schwartz et al., 2003; Schwartz & Purves, 2004). The frequency of the periodic repetitions is measured in Hertz (Hz), which equals cycles per second. Pitch is considered the perceptual correlate of this repetition rate (McDermott & Oxenham, 2008; Oxenham, 2013): The faster the repetition rate, the higher a sound is generally perceived. However, pitch perception is also influenced by other physical properties, e.g., the sound intensity and the overtone structure in complex tones, so that no simple one-to-one mapping between physical and perceptual attributes exists (Fletcher, 1934; Lichte & Gray, 1955).

Most musical tones are harmonic complex tones (Oxenham, 2012; Plack & Oxenham, 2006). Unlike pure tones, which consist of a single sinusoidal waveform, complex tones consist of a combination of multiple sinusoidal waveforms. In harmonic complex tones, the higher frequency partials, called overtones, are integer multiples of the lowest frequency partial, the fundamental frequency F0 (McDermott & Oxenham, 2008; Oxenham, 2012, 2013; Plack et al., 2014; Plack & Oxenham, 2006). The pitch of a harmonic complex tone is usually derived from its fundamental frequency (Oxenham, 2013; Plack et al., 2014). The fundamental pitch is often even perceived when the fundamental frequency of a tone is spectrally missing or masked by interfering sounds (Fletcher, 1924; Licklider, 1956; Schouten, 1938). The pitch percept then corresponds to the greatest common factor of the harmonic overtones. Depending on individual pitch-perception preferences, some listeners predominantly hear the implied pitch of the missing fundamental, while other listeners predominantly hear the spectral pitch of the present overtones (Ladd et al., 2013; Schneider et al., 2005; Schneider & Wengenroth, 2009). Interindividual differences also exist in other dimensions of pitch perception, such as the acuity of pitch discrimination or sensitivity to pitch direction. For instance, musicians can detect smaller differences between pitches compared to non-musicians (Kishon-Rabin et al., 2001; Micheyl et al., 2006; Spiegel & Watson, 1984). On the other hand, people with congenital amusia show deficits in both detecting pitch changes and identifying the direction of pitch changes, i.e., whether a pitch is higher or lower compared to a previous one (Foxton et al., 2004; Peretz et al., 2002). Other people can discriminate pitches well but demonstrate difficulties in determining the direction of the pitch change (Semal & Demany, 2006).

Following the definition given above, pitch lies on a one-dimensional continuum from low to high. However, tones separated by a doubling of the tone frequency tend to be perceived as very similar to each other — sometimes even more similar than tones that are physically closer together on the frequency continuum (Deutsch, 1978; Deutsch & Boulanger, 1984; Moerel et al., 2015; Shepard, 1982). This perception of similarity for doubled frequencies can be observed from infancy on (Demany & Armand, 1984) and was even reported to occur in monkeys and rats (Blackwell & Schlosberg, 1943; Wright et al., 2000). In the musical context, the interval resulting from the doubling of frequency is known as an octave. The octave is used as the basis for most musical scales (Burns, 1999).

In almost all Western music, the octave is subdivided into 12 discrete categories, each a semitone apart. This is referred to as the chromatic scale. In the predominant tuning system, the 12 categories are logarithmically equally spaced by 100 cents each.

Assuming octave circularity, pitch can be considered two-dimensional. The first dimension, pitch height, correlates with the tone frequency (Burns, 1999). The second dimension, pitch chroma, refers to "the underlying quality of any tone and the tones in octave periodicity with it" (Bachem, 1937, p. 147). All tones that are an octave or multiple octaves apart share the same chroma quality and belong to the same pitch class. Pitch classes are labelled with an alphabetical letter to indicate their relative position within the octave (e.g., A). To specify the octave of a pitch, scientific music notation adds an integer to the letter (e.g., A4) (Young, 1939).

The octave circularity and the equal spacing of semitones allow to shift a melody to another tone frequency without changing the musical intervals or affecting melody recognition (Krumhansl, 2000; Levitin & Rogers, 2005). Accordingly, the relative distances between the pitches are far more important to music than the absolute values of the pitches (Krumhansl, 2000; Miyazaki & Rakowski, 2002). And still, AP possessors are somehow uniquely able to label and/or produce such absolute pitch values directly without relying on pitch relationships.

1.2 Absolute Pitch (AP)

As discussed above, music is largely built upon pitch relationships. Most people can discern such pitch relationships but not the absolute values of the pitches; they perceive pitch in relative rather than absolute terms (Plantinga & Trainor, 2005). Highly trained musicians additionally learn to identify the extent of the relative distance between pitches on the musical scale in terms of musical intervals (e.g., major third) (Levitin & Rogers, 2005; Miyazaki, 1990, 2004a; Zatorre et al., 1998). Owing to this accurate relative pitch (RP) ability, most trained musicians are able to reconstruct the label of a pitch when presented with a reference pitch (Athos et al., 2007; Levitin & Rogers, 2005). Only individuals with AP, however, can directly access memory codes for absolute pitch values.

Sometimes, color recognition — easy and immediate for most people — is used as an analogy for the effortlessness with which AP possessors recognize pitches (e.g., Bachem, 1955; Deutsch, 2002; Ward, 1999). Absolute and relative pitch can be understood as two different modes of pitch processing (Miyazaki, 2004a). While musicians with AP may possess some RP skills (see also: Benguerel & Westdal, 1991), they seem to predominantly perceive pitches in absolute terms (Miyazaki, 2004a; Miyazaki & Rakowski, 2002).

Sometimes, AP is misleadingly referred to as "perfect pitch". Contrary to the meaning implied by this layman term, most AP musicians do not demonstrate perfect accuracy in pitch-identification tests. Quite frequently, they are wrong about the pitch height (so-called octave errors) or err by one semitone, either consistently in one direction or randomly (Bachem, 1955; Deutsch, 2013; Lockhead & Byrd, 1981; Miyazaki, 1988, 1989; Takeuchi & Hulse, 1993). Pitch-identification performance is also strongly affected by various stimulus features and by no means perfect across all periodic sounds (for more details, see Section 1.2.4 Behavioral Characteristics). Moreover, AP is not necessarily accompanied by exceptional low-level auditory processing as it is often assumed (Deutsch, 2013). In fact, AP musicians show similar resolutions for frequency, temporal, and spatial differences in sounds as non-AP musicians (Fujisaki & Kashino, 2002; Sergeant, 1969).

1.2.1 Operational Definition

Despite a general agreement on the verbal definition of AP, the scientific community has not yet reached a consensus on an operational definition. A variety of methods and criteria are used to identify AP possessors (for a detailed overview, see Takeuchi & Hulse, 1993). In most studies, AP classification is based either on self-report (e.g., Athos et al., 2007; Baharloo et al., 1998; Zatorre & Beckett, 1989), pitch-identification tasks (e.g., Deutsch et al., 2009; Miyazaki, 1988; Miyazaki et al., 2018), pitch-production/-adjustment tasks (e.g., Dohn et al., 2014; Ross et al., 2005; Wenhart et al., 2019), or any combination thereof. Pitch-identification tasks are the most common to behaviorally verify AP (Bermudez & Zatorre, 2009), but they vary greatly in procedure. To date, no standard has been established for the stimulus material (e.g., timbre of tones, stimulus duration, pitch

register, number of different tones), the trial construction (e.g., trial duration, answer registration, intermittent interference stimuli), the test administration (e.g., web-based or on-site, degree of automation, number of trials), the scoring procedure (e.g., full or partial points for octave and semitone errors, inclusion of response latency information, inclusion of variability information), or the performance criteria to classify someone as AP possessor (e.g., varying cutoffs for the percentage of correct trials). The lack of standardized measures may account for some of the heterogeneity of the results in studies on AP.

1.2.2 Prevalence and Distribution

The phenomenon of AP has fascinated laymen and researchers alike, not least because of its perceived rarity. In the general population, the incidence of AP has been estimated at 0.07 % (Profita & Bidder, 1988) or less than 0.01 % (Bachem, 1955). While these numbers are commonly cited in the literature, they have not yet been backed by robust empirical evidence. The original estimates were inferred from unpublished observations using biased samples and undisclosed AP criteria (Leite et al., 2016; Miyazaki et al., 2012). Assessing the true occurrence rate of AP in the general population remains challenging, as most testing methods and definition criteria require knowledge of the chromatic scale. The prevalence among musicians has been investigated more thoroughly. In Europe and the Americas, AP seems to occur in about 4–15 % of musicians, depending on the sampling and the criteria (Baharloo et al., 1998; Chavarria-Soley, 2016; Gregersen et al., 1999, 2001; Leite et al., 2016; Miyazaki et al., 2012). In East Asia, AP appears to be more prevalent among musicians than in Western countries. A recent large-scale study (Miyazaki et al., 2018) tested musicians in five countries (Japan, China, Poland, Germany, USA). With a criterion of 90 % correctly identified tones (octave position was not required), the prevalence estimates ranged from nearly 0 % to 12 % for the Western Countries. For the East Asian countries, the prevalence was much higher with estimates between 8 % and 57 %, substantiating previous reports (Deutsch et al., 2006, 2013; Miyazaki et al., 2012).

Although prevalence estimations seem to proceed on the assumption that AP possessors are a distinct population, there is not yet a community-wide agreement on whether AP

should be treated as a dichotomous or as a gradual ability. It is not unusual that a considerable proportion of musicians scores between chance level and near-perfect acuity in pitch-identification tasks. To account for intermediate levels and intra-individual variations (e.g., based on testing material), different subtypes of AP have been proposed. According to an influential classification put forward in 1937 by Bachem, an AP possessor himself, *genuine* AP is present when the pitch chroma of a tone is immediately recognized (Bachem, 1937). The pitch height (octave designation), on the other hand, is not necessarily better recognized than in the absence of AP. Genuine AP can be either universal for most instruments and octave ranges, limited to certain instruments and/or octave ranges, or even inaccurate and variable. Genuine AP is to be differentiated from *Quasi*-AP. Musicians with Quasi-AP do not show immediate recognition of pitches but can still perform well in pitch-identification tasks. They use a single internalized aural or vocal reference pitch (e.g., the standard A) in combination with well-developed RP skills to determine a pitch in isolation (Bachem, 1937). In that sense, Quasi-AP can be interpreted either as AP for a single tone (Levitin & Rogers, 2005) or as very proficient RP (Leipold, 2019). Other subtypes that have been proposed include *partial* AP for white key notes only (Miyazaki, 2004a) or *absolute piano* for piano tones only (Ward, 1999). Due to the varying degrees of AP proficiency, it has been suggested that AP is not a binary trait but rather falls on a continuum from completely absent AP to practically perfect AP (Levitin & Rogers, 2005; Vitouch, 2003). Several studies have observed a relatively continuous distribution of AP scores in their samples, supporting this view (e.g., Baharloo et al., 1998; Bermudez & Zatorre, 2009; Chavarria-Soley, 2016; Wilson et al., 2012). On the other hand, a large-scale study with 2,213 participants conducted by Athos et al. (2007) found a clear bimodal distribution of the pitch-identification scores. To prevent the use of RP strategies, which might partially account for intermediate performances, Wengenroth et al. (2014) designed a pitch-identification task with intermittent non-harmonic and distorted interference stimuli. Like Athos et al. (2007), they found a bimodal distribution in their sample of 162 musicians, supporting a dichotomous view of AP. However, there was still a high variability of the pitch-identification scores. It is possible that — in line with Bachem's characterization of genuine AP (Bachem, 1937) — AP is indeed gradual but only within the distinct population of (genuine) AP possessors (Leipold, 2019; Wengenroth et al., 2014; compare also Van Hedger et al., 2020).

1.2.3 Development

Because the ability of AP is viewed as unique and desirable by many, its genesis has naturally received considerable attention. Early in the history of AP research, two (supposedly) opposing viewpoints were advocated: heredity and learnability (for an overview, see Ward, 1963, 1999).

A genetic component is strongly suggested by the familial aggregation of AP (Bachem, 1940, 1955; Baharloo et al., 1998, 2000; Gregersen et al., 1999, 2001; Profita & Bidder, 1988; Theusch et al., 2009) — an effect that persists even when controlling for early musical training, which in itself also tends to cluster in families (Baharloo et al., 2000). What is more, in a twin study the concordance rate for AP was significantly higher in identical twins than in non-identical twins (Theusch & Gitschier, 2011). A second argument for a genetic contribution is that AP usually manifests at a very young age before any extensive musical training took place (e.g., Bachem, 1955; Profita & Bidder, 1988). Consequently, having AP is so natural to many AP possessors that they are initially astonished to learn that not everyone has it (Profita & Bidder, 1988; see also Deutsch, 2013). A third argument in favor of a genetic influence is the phenotypic and genetic overlap between AP and synesthesia (Gregersen et al., 2013), another rare perceptual phenomenon that seems to run in families (Barnett et al., 2008; Baron-Cohen et al., 1996). AP also appears to be more prevalent in populations with certain genetic-based conditions, such as Williams syndrome (Lenhoff et al., 2001; but see Martínez-Castilla et al., 2013) and autism spectrum disorders (Heaton et al., 1998). The exact genetic basis of AP is, however, still poorly understood. As of yet, two genome-wide linkage studies have identified several genes that might be associated with AP (Gregersen et al., 2013; Theusch et al., 2009), and one potential candidate gene has been proposed (Gregersen et al., 2013). Evidence from genetic segregation analyses further indicates that AP is genetically heterogenous (Theusch et al., 2009; Theusch & Gitschier, 2011).

The most extreme form of the *learnability* theory was antithetical to the heredity viewpoint (Ward, 1999); AP can be acquired by anyone at any time during life independently of a genetic predisposition, given the right circumstances and experiences. However, learning AP does not seem to be as straightforward as implied by this view. Early attempts to acquire AP through practice in adulthood were mostly unsuccessful or

required an enormous amount of effort (for an overview, see Deutsch, 2013; Ward, 1999). This stands in marked contrast to the effortless acquisition in childhood without deliberate practice that many AP possessors report (Deutsch, 2013; Profita & Bidder, 1988). Furthermore, it has repeatedly been observed that the prevalence of AP is higher in musicians who started musical training early in life, and that the accuracy in pitch identification is negatively correlated with the age of onset of musical training (e.g., Baharloo et al., 1998, 2000; Deutsch et al., 2006, 2009; Gregersen et al., 1999; Lee & Lee, 2010). These observations gave rise to the *early learning* theory, which postulates that anyone can learn AP but only during a critical period in life (Takeuchi & Hulse, 1993). This critical period was suggested to be analogous to the critical period in language acquisition (Deutsch, 2002). As Levitin and Zatorre (2003) clarified, this does not imply that no one can learn AP later in life; based on the assumption of a normal distribution of the critical period, it is very well possible that a few outliers exist. However, going beyond what would be expected, three recent studies reported successful acquisition of AP in a relatively large proportion of their adult samples through specific training protocols (Van Hedger et al., 2019: 33 %; Wong, Lui, et al., 2020: 14 %; Wong, Ngan, et al., 2020: 15 %). Consequently, Van Hedger et al. (2019) proposed the *skill acquisition* theory, which states that some (but not all) individuals can indeed acquire high AP levels at any age by following specific training protocols. Early musical exposure might nonetheless be one of the prerequisites for the AP training to work (Van Hedger et al., 2019). In all three studies (Van Hedger et al., 2019; Wong, Lui, et al., 2020; Wong, Ngan, et al., 2020), the successfully trained participants had previous musical experience. This in turn highlights another important aspect of the critical period: not all individuals who receive musical training during the critical period develop AP. Early musical training may be necessary but is not sufficient; a genetic predisposition and/or other environmental experiences are additionally required.

Such other potential factors in the acquisition of AP were discussed in the context of the above-mentioned (see Chapter 1.2.2 Prevalence and Distribution) high prevalence of AP in East Asian musicians (Gregersen et al., 1999, 2001, 2007; Henthorn & Deutsch, 2007). The prevalence difference to Western musicians might in part be explained by different types of musical trainings. In East Asia, the so-called *fixed-do* aural training is quite common, whereas the so-called *moveable-do* training is widespread in some of the

Western countries with a low AP prevalence (e.g., in England and the USA; Deutsch, 2013). In the fixed-do system, each solfège syllable (do, re, mi, etc.) corresponds to one specific pitch (e.g., do is always C). In the movable-do system, the solfège syllables are not tied to specific pitches but rather define the relative distance to the first note of the scale, called the tonic. Early fixed-do training is thought to facilitate the acquisition of AP (Gregersen et al., 2001, 2007; see also Wilson et al., 2012). However, even in the absence of early musical training, Asian musicians seem to have a higher probability than Western musicians for having AP (Gregersen et al., 2001; Miyazaki et al., 2018). Thus, the training method alone cannot explain the prevalence difference. Another explanation that has been offered is the exposure to tone languages (Deutsch, 2002; Deutsch et al., 2004, 2006, 2009). In tone languages, the pitch of the voice and the pitch contour can completely change the meaning of a word, not only add subtle nuances as in most languages (Yip, 2002). For example, the Cantonese word [yau] can mean “oil” or “worry” (among others) depending on the pitch it is spoken with. Like in AP, the pitch is associated with a verbal label. Exploring the stability of pitch in speech, Deutsch et al. (2004) found that the pitch of words enunciated by native Vietnamese and Mandarin speakers was precise and stable across different days. Native English speakers, on the other hand, were not as consistent in their enunciation. The authors hypothesized that being exposed to a tone language in infancy might enable the formation of a neural circuit for pitch-label associations that also underlies AP (Deutsch et al., 2004). Later, Deutsch and Dooley (2013) found that AP possessors can hold more auditory (but not visual) digits in memory than non-AP possessors. They speculated that a large auditory memory span might facilitate the development of AP, which could explain why some non-tone language speakers still develop AP. Indeed, in another study, the working memory capacity predicted how well adult non-AP possessors learned AP note categories in a single session (Van Hedger, Heald, Koch, et al., 2015). Also, the two adult non-tone language speakers who successfully acquired AP after a 20-hour long AP training had the best pre-training tonal working memory out of all study participants (Wong, Ngan, et al., 2020). It, however, remains unclear whether the development of true AP (i.e., early and effortlessly acquired) depends on the same mechanisms as training AP in adulthood (Van Hedger, Heald, Koch, et al., 2015).

In summary, contrary to the early debate, it now seems likely that both genetic and environmental factors contribute to the development of AP. Because it is a relatively isolated ability, AP was even proposed as a candidate model for investigating how genes and environment interact in the emergence of cognitive functions in general (Zatorre, 2003). On the other hand, telling apart the genetic and environmental influences on AP remains difficult precisely because of these interactions. For example, someone who has a high genetic predisposition for AP might also be more inclined to start musical training early in life (Gregersen et al., 1999). Furthermore, it is inherently challenging to tease out the innate components of an ability that by definition requires musical knowledge and, thus, musical training (Levitin & Rogers, 2005).

1.2.4 Behavioral Characteristics

One of the main features of AP is its effortlessness. Pitch identification in AP is rapid (e.g., Bachem, 1937; Bermudez & Zatorre, 2009; Miyazaki, 1990; Wilson et al., 2009), reflecting the ease with which AP musicians can access the labels corresponding to the pitches. The cognitive process of assigning memory codes (e.g., labels) to pitches in AP has even been described as involuntary and automatic (Levitin & Rogers, 2005; Miyazaki & Rakowski, 2002). Empirically, the automaticity of AP has mainly been studied by means of auditory Stroop tasks (Akiva-Kabiri & Henik, 2012; Hsieh & Saberi, 2008; Itoh et al., 2005; Miyazaki, 2004b; Schulze et al., 2013). Typically, AP musicians show increased response times for the naming of visual notes or sung tone labels when simultaneously confronted with an incongruent pitch. This behavioral incongruence effect indicates that pitch labeling is difficult to suppress for AP musicians even if it is disadvantageous for the present task. It has also been suggested that the tendency to rely on AP might hinder the performance in some RP tasks. Musicians with AP were shown to experience more difficulties in identifying musical intervals in an out-of-tune context compared to an in-tune context (Miyazaki, 1992, 1993), and in recognizing atonal melodies when they were transposed (Miyazaki & Rakowski, 2002). However, as pointed out by Dooley and Deutsch (2010, 2011), these findings could also be interpreted as Stroop-like interference effects under artificial conditions rather than a general disadvantage of AP in RP tasks.

Despite the presumed high degree of automaticity and the absolute nature of AP, pitch-identification performance in AP musicians varies greatly depending on a range of stimulus- and context-specific factors. For instance, both the accuracy and the speed of pitch identification are affected by the timbre of the stimulus (Gruhn et al., 2019; Lee & Lee, 2010; Lockhead & Byrd, 1981; Marvin & Brinkman, 2000; Miyazaki, 1989; Schlemmer et al., 2005; Van Hedger & Nusbaum, 2018; Vanzella & Schellenberg, 2010; Wong & Wong, 2014): For most AP musicians, instrumental tones are easier to identify than pure tones (e.g., Gruhn et al., 2019; Miyazaki, 1989), and non-vocal stimuli seem to be better recognized than vocal stimuli (Vanzella & Schellenberg, 2010). Familiarity with a timbre, such as the timbre of the primary instrument, might additionally facilitate pitch identification (Krumhansl, 2000; Lockhead & Byrd, 1981; Miyazaki, 1989; Takeuchi & Hulse, 1993). Also, pitches within unfamiliar octave ranges may be more difficult to identify than within familiar octave ranges (Takeuchi & Hulse, 1993). In general, pitches of central registers, which are most common in music, are more accurately identified than those of very high or very low registers (Miyazaki, 1989). Additionally, performance seems to depend on the pitch class: Identification of white keys has repeatedly been shown to be more accurate and quicker than identification of black keys (Athos et al., 2007; Bermudez & Zatorre, 2009; Chavarria-Soley, 2016; Deutsch et al., 2013; Gruhn et al., 2019; Leite et al., 2016; Miyazaki, 1988, 1990; Miyazaki et al., 2012; Takeuchi & Hulse, 1991). One study also reported a higher accuracy in a pitch-adjusting task for white keys than for black keys (Dohn et al., 2014).

Apart from the stimulus itself, AP is also influenced by the context the stimulus appears in (Hedger et al., 2013; Van Hedger et al., 2018; Van Hedger, Heald, & Nusbaum, 2015). This was impressively demonstrated in a study by Hedger et al. (2013). They let proficient AP possessors listen to musical pieces (45–60 minutes long) which were slowly detuned to 1/3 semitone flat within the first 15 minutes. In the subsequent intonation judgments of isolated tones, the AP musicians' perception was likewise shifted in the flat direction. More recently, Van Hedger et al. (2018) could demonstrate that the listening context can also modify intonation judgments and pitch categorizations within a much shorter time span of only a few seconds. In another study, Van Hedger et al. (2015) found that AP possessors were slower in detecting a target tone when it was presented in an acoustic context with increased variability (i.e., among tones from different instruments or from

different octaves), again confirming that AP is not entirely independent of the listening context. Furthermore, the internal pitch templates can also be reinforced or destabilized by one's own recent musical activity, such as the current amount of musical training or ongoing exposure to a fixed-do/moveable-do instrument (Dohn et al., 2014; Wilson et al., 2012).

Changes in pitch perception of AP possessors do not only occur in response to external situational factors but also in response to personal factors. For instance, Athos et al. (2007) found a gradual perceptual shift in the sharp direction with advancing age, substantiating previous anecdotal reports (Profita & Bidder, 1988; Vernon, 1977; Wynn, 1992). There is also anecdotal evidence from two female AP possessors that fluctuations in AP measures are related to the menstrual cycle (Wynn, 1973). Furthermore, pitch-identification performance might also be affected by internal states, such as fatigue and motivation. In a single case study, the AP subject mentioned changes in pitch perception due to fatigue (Chaloupka, 1994). In another study, approximately one third of the participants reported that fatigue interferes with their AP ability (Profita & Bidder, 1988).

Taken together, AP is behaviorally characterized by short response times and high accuracy in pitch-chroma identification, but also by a high variability in performance measures based on the stimulus and the context. The dependence on external, internal, and age-related factors indicates that the internalized pitch categories in AP are not as fixed as was long assumed (see e.g., Ward, 1999). Finally, interference effects suggest that pitch labeling in AP is highly automatic.

1.2.5 Cognitive Architecture

Given that AP possessors are not superior in basic hearing abilities (see Chapter 1.2 Absolute Pitch (AP); Fujisaki & Kashino, 2002; Sergeant, 1969), the question arises of what perceptual and/or cognitive processes enable them to so accurately identify and produce isolated pitches. One of the underlying mechanisms that has been suggested is categorical perception for tone frequency (Harris & Siegel, 1975; Rakowski, 1993; Siegel & Siegel, 1977). Categorical perception describes the phenomenon that a continuous variable is perceived in categories in such a way that changes along the continuum are

more difficult to discern within than between categories. However, it was later found that AP musicians can discriminate pitches well within categories and do not show the typical sharp cross-category boundaries (Levitin & Rogers, 2005). The hypothesis that AP possessors have a better short-term or echoic memory for tones could also be refuted. In pitch-recognition and pitch-recall tasks, their memory decay within the first few seconds is comparable to that of non-AP possessors (Bachem, 1954; Rakowski, 1972; Siegel, 1974). For longer retention intervals, on the other hand, the decline in performance is less pronounced in AP possessors than in non-AP possessors. Siegel (1974) concluded that AP possessors can use verbal note names instead of sensory traces to encode and remember the note after echoic memory has faded. The use of such codes in AP is supported by the fact that the task performance of AP possessors is worse for pitches that fall in-between pitch categories (Rakowski, 1972). Furthermore, AP possessors are not better than non-AP possessor at remembering extremely high frequencies, which cannot be assigned to one definite pitch class (Bachem, 1954). Importantly, the coding of the pitch class probably need not be verbal; rather AP possessors can use different codes, such as kinesthetic or visual imagery (Zatorre & Beckett, 1989; but see Takeuchi & Hulse, 1993 for limitations of the finding). To retrieve the verbal or nonverbal code, AP possessors presumably compare the pitch of an incoming sound to internalized pitch templates associated with fixed pitch labels (see also Lockhead & Byrd, 1981; Ward, 1963, 1999; Zatorre & Beckett, 1989). The capacity to access such pitch templates might also explain the reduced working memory load in AP possessors in other tasks (e.g., Hantz et al., 1992; Itoh et al., 2005; Klein et al., 1984; Wayman et al., 1992; Zatorre et al., 1998).

Zatorre (2003) hypothesized that in addition to an associative memory component for labeling, AP also requires a refined perceptual encoding ability. Pitches are first placed into particularly narrow pitch categories, and then, these categories are associated with verbal labels or other codes. By contrast, the influential two-component model proposed by Levitin (1994; Levitin & Rogers, 2005) assumes that the lower levels of tone processing do not differ between listeners with and without AP. Instead, the importance of higher-level processes is emphasized. Expanding on the idea of internal pitch templates (e.g., Ward, 1963), the model posits that two distinct abilities are involved in AP: first, maintaining and accessing long-term memory representation of pitches (*pitch memory*), and second, associating these representations with linguistic labels (*pitch labeling*). While

only individuals with AP would have both traits, pitch memory is thought to be widespread even among non-AP possessors (Levitin, 1994). Several findings support such a latent form of AP. In a series of experiments, Terhardt and Seewann (1983) — replicating and extending a previous exploratory study (Terhardt & Ward, 1982) — played musically trained participants short excerpts from Bach preludes in either the original key or in one of several transposed keys. They found that the majority of the participants who claimed to not have AP could distinguish whether the excerpt was played in its original tune or was detuned by up to 4 semitones. Almost half of the participants were able to identify a detuning of 1 semitone. Other studies have shown that even non-musicians can recognize small pitch shifts of familiar songs (Schellenberg & Trehub, 2003, 2008), of the landline dial tone (Smith & Schmuckler, 2008), or of the 1000-Hz censor tone in broadcast media (Van Hedger et al., 2016). Beyond recognition, non-AP possessors can also hum or sing familiar songs with little variance in the starting pitch on separate days (Bergeson & Trehub, 2002; Halpern, 1989). In Levitin's (1994) own study on this topic, almost half of the participants were able to produce (i.e., hum, sing, or whistle) two well-known contemporary songs within 2 semitones of the original pitch (for replications, see Frieler et al., 2013; Jakubowski & Müllensiefen, 2013). Overall, these findings suggest that people without AP may also store some stable pitch representations. Therefore, the ability to associate these long-term representations with labels is what sets AP possessors apart from non-possessors according to the two-component model (Levitin, 1994). Importantly, the comparison to the internal pitch template is thought to occur automatically after the pitch was extracted from the tone (Levitin & Rogers, 2005).

Contrary to the two-component model and most other models of AP, including those pertaining to the development of AP, Ross et al. (2005) argued that AP is relatively independent of pitch labeling and musical training. Based on testing methods that do not require knowledge of note names, they differentiated between two types of AP with different underlying mechanisms: APE, the ability to encode the absolute frequency of acoustic stimuli at an early perceptual stage; and HTM (heightened tonal memory), the enhanced ability to memorize and retrieve specific complex tones. While Ross et al.'s (2005) suggestion of a more inclusive definition of AP is reasonable, it has not yet led to a change in practice in AP research. The prevailing view is that AP is a musical phenomenon.

1.3 Aims

Most of the current knowledge about AP comes from behavioral studies. Neuroscientific research can help further improve our understanding of the phenomenon by shedding light on the underlying neural and cognitive mechanisms. This is nicely illustrated by the very first AP study reporting differences in event-related potentials (ERPs). The P3b, a subcomponent of the P300, was found to be reduced or even absent in AP possessors when they had to count the rarer of two stimuli in an auditory oddball task (Klein et al., 1984). The P3b is typically elicited by the rare stimulus and presumably reflects the updating of working memory. The finding suggests that AP possessors rely less on working-memory processes than non-AP possessors to identify the rare stimulus — possibly because they have access to permanent pitch templates and do not need to compare sounds to detect a novel stimulus (Klein et al., 1984). Even though the behavioral performance (i.e., accuracy of counting) was similar in the two groups, the differences in EEG measures successfully provided new insights into the underlying cognitive processes of AP. Other studies have focused on the brain regions that contribute to AP. Using positron emission tomography (PET), one influential study showed that the left dorsolateral prefrontal cortex (DLPFC) might be involved in the often-postulated spontaneous association of pitches with verbal labels in AP (Zatorre et al., 1998). Another seminal study, the first to suggest neuroanatomical differences in AP, implicated the planum temporale (PT), a non-primary auditory region posterior to the Heschl's gyrus, in AP (Schlaug et al., 1995).

Despite the great potential of cognitive neuroscience, our understanding of how AP is represented in the brain is still very limited. Compared to behavioral research, research into the neural bases of AP is a relatively new field, and it is considerably more resource intensive. As a consequence, the number of neuroscientific studies on AP is still small in comparison, and most of the studies have been conducted with small samples. Small sample sizes are problematic because they can lead to low statistical power, which in turn increases the chance of missing a true effect and decreases the probability that a statistically significant finding reflects a true effect (Button et al., 2013). This could at least in part explain why previous neuroscientific studies yielded inconsistent results. To get

more robust results for a more profound understanding of the neural underpinnings of AP, studies with larger samples are imperative.

The overarching aim of the current thesis was to extend our knowledge about neurophysiological features of AP by studying a large sample of musicians. We compared the electrophysiological activity of musicians with and without AP under three different experimental conditions: passive tone listening, resting state, and an auditory Go/Nogo task. All three experimental conditions had in common that they did not require explicit pitch labeling.

In article 1, we aimed to re-examine whether the assumed automaticity of AP affects pitch processing during passive listening. Replicating a previous study (Rogenmoser et al., 2015), we analyzed two ERP components in a passive auditory oddball paradigm: the mismatch negativity (MMN), which reflects pre-attentive memory processes, and the P3a, which reflects early attentional processes. In the original study, AP musicians showed a similar MMN amplitude as non-AP musicians but a smaller P3a amplitude. This suggests that early cognitive processes in AP musicians are more efficient not only during attentive listening (e.g., reduced P3b in active oddball: Klein et al., 1984) but even during passive listening. By contrast, pre-attentive auditory processes may be less important to AP.

To further assess the role of perceptual and cognitive processes in AP, article 2 re-evaluated and explored the contributions of sensory and higher-order brain areas to AP networks at rest. The first part of the study describes a replication attempt of a previous finding of increased theta connectivity in AP musicians between the left auditory cortex and the left DLPFC (Elmer et al., 2015). We aimed to test the robustness of this finding by using a larger sample of musicians and a wider variety of connectivity measures. In the second part of the study, we performed an exploratory whole-brain analysis to find out which additional regions are potentially involved in a more widespread functional AP network.

In article 3, we used an auditory Go/Nogo task to investigate the extent of automaticity of AP processes. Previous studies have shown that AP can interfere with task demands indicating that pitch labeling in AP is difficult to suppress. Furthermore, AP possessors

sometimes show increased neurophysiological activity in response to tones compared to non-AP possessors even when they were not explicitly instructed to label the pitches. Using two different Nogo conditions, we tested if the inhibitory load in the Go/Nogo task is affected by the presumably automatic pitch labeling in a Stroop-like manner and/or by the generally stronger neurophysiological response to acoustic stimuli.

Chapter 2 Empirical Work: Article 1

Electrophysiological correlates of absolute pitch in a passive auditory oddball paradigm: a direct replication attempt

Marielle Greber, Lars Rogenmoser, Stefan Elmer, Lutz Jäncke

Abstract

Humans with absolute pitch (AP) are able to effortlessly name the pitch class of a sound without an external reference. The association of labels with pitches cannot be entirely suppressed even if it interferes with task demands. This suggests a high level of automaticity of pitch labeling in AP. The automatic nature of AP was further investigated in a study by Rogenmoser et al. (2015). Using a passive auditory oddball paradigm in combination with electroencephalography, they observed electrophysiological differences between musicians with and without AP in response to piano tones. Specifically, the AP musicians showed a smaller P3a, an event-related potential (ERP) component presumably reflecting early attentional processes. In contrast, they did not find group differences in the mismatch negativity (MMN), an ERP component associated with auditory memory processes. They concluded that early cognitive processes are facilitated in AP during passive listening and are more important for AP than the preceding sensory processes.

In our direct replication study on a larger sample of musicians with (n = 54, 27 females, 27 males) and without (n = 50, 24 females, 26 males) AP, we successfully replicated the non-significant effects of AP on the MMN. However, we could not replicate the significant effects for the P3a. Additional Bayes factor analyses revealed moderate to strong evidence (Bayes factor > 3) for the null hypothesis for both MMN and P3a. Therefore, the results of this replication study do not support the postulated importance of cognitive facilitation in AP during passive tone listening.

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Cognition and Behavior

Electrophysiological Correlates of Absolute Pitch in a Passive Auditory Oddball Paradigm: a Direct Replication Attempt

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Abstract

Humans with absolute pitch (AP) are able to effortlessly name the pitch class of a sound without an external reference. The association of labels with pitches cannot be entirely suppressed even if it interferes with task demands. This suggests a high level of automaticity of pitch labeling in AP. The automatic nature of AP was further investigated in a study by Rogenmoser et al. (2015). Using a passive auditory oddball paradigm in combination with electroencephalography, they observed electrophysiological differences between musicians with and without AP in response to piano tones. Specifically, the AP musicians showed a smaller P3a, an event-related potential (ERP) component presumably reflecting early attentional processes. In contrast, they did not find group differences in the mismatch negativity (MMN), an ERP component associated with auditory memory processes. They concluded that early cognitive processes are facilitated in AP during passive listening and are more important for AP than the preceding sensory processes. In our direct replication study on a larger sample of musicians with (n = 54, 27 females, 27 males) and without (n = 50, 24 females, 26 males) AP, we successfully replicated the non-significant effects of AP on the MMN. However, we could not replicate the significant effects for the P3a. Additional Bayes factor analyses revealed moderate to strong evidence (Bayes factor $>$ 3) for the null hypothesis for both MMN and P3a. Therefore, the results of this replication study do not support the postulated importance of cognitive facilitation in AP during passive tone listening.

Key words: absolute pitch; auditory; ERP; MMN; P3a; replication

Significance Statement

A better understanding of the neural basis of absolute pitch (AP), the ability to identify a pitch without an external reference, provides valuable insights to the mechanisms of pitch processing in the human brain. Since only a tiny fraction of the population possesses AP, most previous neuroscientific research had small sample sizes. In our direct replication, we used a large sample of musicians (n = 104) with and without AP to confirm an intriguing finding showing that AP musicians process tones more efficiently even when not actively attending them. Using both frequentist and Bayesian analyses, we failed to replicate this effect with an identical experimental setting. This finding highlights the significance of replications and the need for large sample sizes.

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Introduction

Replications are an integral part of science. They can help estimate the size of an effect, identify the specific conditions under which it occurs, and, when successful, increase confidence in a scientific claim (Nosek et al., 2012; Brandt et al., 2014). In recent years, the low replicability of published research has become an increasing concern within neuroscience and science in general (Baker, 2016). Possible explanations for the observed low replicability include publication bias, flexibility in data analysis, and low statistical power (Munafò et al., 2017). Due to the resource-intensive data acquisition, many neuroscientific studies use small sample sizes, resulting in low power (Szucs and Ioannidis, 2017). Low power can compromise the conclusions of a study by reducing the probability of detecting a true effect, by increasing the probability that a significant finding does not reflect a true effect, and by overestimating the size of an effect (Button et al., 2013).

Acquiring data from a large sample is even more challenging for studies investigating special populations like individuals with absolute pitch (AP), the rare ability to label the pitch class (chroma) of a sound without an external reference (Takeuchi and Hulse, 1993; Zatorre, 2003; Levitin and Rogers, 2005). AP is often contrasted with relative pitch (RP), the more common ability to identify the musical interval (pitch distance) between two tones (McDermott and Oxenham, 2008). Despite its rarity, AP has received considerable scientific attention, partly because it might help understand different modes of perceptual processing and general aspects of pitch memory (Levitin and Rogers, 2005).

The neural and cognitive mechanisms underlying AP are not yet fully understood, but several studies have demonstrated that the labeling process in AP is at least in part automatic and not suppressible, even if it is disadvantageous for the task at hand (Miyazaki and Rakowski, 2002; Itoh et al., 2005; Schulze et al., 2013). The extent of this automaticity was further investigated by studies recording the electroencephalogram (EEG) during passive listening (Tervaniemi et al., 1993; Elmer et al., 2013; Matsuda et al., 2013; Rogenmoser et al., 2015). Using this approach, one can study the neurophysiological correlates of the automatic labeling process with high temporal resolution while minimizing the influence of top-down processes.

An often-used paradigm is the passive auditory oddball, in which one tone (standard) is presented more frequently than the other tones. The infrequent tones (deviants) are known to reliably elicit two frontal event-related potential (ERP) components: the mismatch negativity (MMN) and the P3a. Both ERP components are usually assessed by subtracting the standard ERP from the deviant ERP. The MMN is a negative deflection on this difference wave that peaks around 100–250 ms after stimulus onset and possibly reflects an automatic memory-based detection of change or rule violation (Picton et al., 2000; Garrido et al., 2009; Näätänen et al., 2011). While the MMN is thought to represent pre-attentive processing, the subsequently occurring positive deflection P3a has been linked to involuntary attention shifts toward unattended stimuli (Escera et al., 1998; Friedman et al., 2001; Kujala et al., 2007; Polich, 2007).

Rogenmoser et al. (2015) were the first to analyze both MMN and P3a in AP, which allowed them to study the influence of the sensory and the early cognitive processes reflected by these ERP components. They recorded EEG from 16 AP musicians and 10 non-AP musicians during a passive auditory oddball paradigm. The analysis of the MMN did not reveal any significant group differences, but AP musicians showed smaller P3a amplitudes than non-AP musicians when the deviations were larger than one semitone. The authors concluded that early cognitive processes are more efficient in AP during passive listening, whereas pre-attentive auditory processing contributes less to AP. This is in accordance with theoretical perspectives describing AP as a mainly cognitive ability (Zatorre, 2003; Levitin and Rogers, 2005).

Within small research fields like AP research, every single study has a high impact on the development of theoretical models. At the same time, the sample sizes are often small, which increases the need for replications. Rogenmoser et al. (2015) showed that AP musicians process tones differently even when not actively attending them. The extent of automaticity implied by this is both interesting and surprising. The aim of the present study was to confirm this finding in an independent and larger sample ($n = 104$). We attempted a direct replication, using the same stimuli, measures, and statistical analyses as in the original study. In addition, we calculated Bayes factors to quantify the success of the replication.

Materials and Methods

Participants

The current study was conducted as part of a broader research project on AP, involving multiple experiments using different imaging modalities [magnetic resonance imaging (MRI) and EEG]. Fifty-four self-reported AP possessors and 50 self-reported non-AP possessors be-

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Table 1. Demographics and musical experience

	AP musicians (n = 54)	Non-AP musicians (n = 50)
Sex		
Female	27	24
Male	27	26
Age (years)	26.67 (5.49)	25.30 (4.51)
Handedness		
Right-handed	47	45
Left-handed	4	4
Both-handed	3	1
Intelligence (MWT-B)[a]	27.69 (5.10)	29.06 (4.68)
Age of onset of musical training (years)	5.93 (2.39)	6.48 (2.46)
Lifetime cumulative training (h)[b]	1.66 (1.22)	1.36 (0.96)
Musical aptitude (AMMA)[a]	66.11 (6.31)	63.22 (6.86)
Pitch-labeling test (%)	76.41 (19.55)	24.31 (19.01)

Continuous measures are given as mean (SDs in parentheses). MWT-B, Mehrfachwahl-Wortschatz-Intelligenztest; AMMA, Advanced Measures of Music Audiation.
[a] Raw scores.
[b] Units are given in 1×10^4.

tween the age of 18 and 44 years were recruited for the current study.

All participants were professional musicians, music students, or highly-trained amateur musicians and received payment for their participation. The research protocol was approved by the local ethics committee in accordance with the Declaration of Helsinki, and all participants provided written informed consent.

None of the participants reported any past or present severe neurologic, psychiatric, or audiological disorders. Normal hearing was confirmed by pure-tone audiometry in all participants (MAICO ST 20, MAICO Diagnostic, GmbH). The two groups were matched for sex, age, handedness, age of onset of musical training, and cumulative training hours over the lifespan. Handedness was assessed by self-report and validated by the Annett Handedness Questionnaire (Annett, 1970). To control for possible between-group differences in intelligence, the Mehrfachwahl-Wortschatz-Intelligenztest (MWT-B; Lehrl, 2005) was administered. The MWT-B quantifies verbal intelligence and was shown to be a good predictor of global IQ (Lehrl et al., 1995). The musical aptitudes of the participants were assessed based on the total scores in the Advanced Measures of Music Audiation (AMMA; Gordon, 1989). To estimate musical experience in terms of age of onset of musical training and number of training hours, participants filled out an online questionnaire before taking part in the experiment. Demographical information and information on musical experience are given in Table 1.

Pitch-labeling test

Pitch-labeling ability was estimated using a web-based behavioral test (adapted from Oechslin et al., 2010), in which participants had to identify the pitch class and pitch height of 108 pure tones. The tones ranged from C3 to B5 (tuning: A4 = 440 Hz), lasted 500 ms, and were each presented three times in a pseudorandomized order with no tones repeated immediately in successive trials. In each trial, 2000 ms of Brownian noise was presented immediately before and after the pure tone. Answers were given by clicking on one label out of a list of all 36 possible labels (C3 to B5). Trials lasted 15,000 ms but could be terminated early by clicking on a "next" button. Pitch-labeling ability was determined by the relative frequency of correctly identified tones in terms of pitch chroma and irrespective of octave errors (Miyazaki, 1989, 1988; Takeuchi and Hulse, 1993; Deutsch, 2013).

Table 2. Study design

	Standard tone	Deviant tones			
Block A	440 Hz	438 Hz	422 Hz	416 Hz	264 Hz
Block C	264 Hz	416 Hz	422 Hz	438 Hz	440 Hz

Deviant tones are listed from left to right according to increasing deviation magnitude.

Stimulus material and experimental procedure

Since the current study was a direct replication, we followed the experimental procedure of the original study as closely as possible. The stimulus material and the code for stimulus presentation were identical to those used in the original study. The auditory stimuli consisted of five piano tones with different fundamental frequencies. Three of the tones were in tune (C4 = 264 Hz, A4 = 440 Hz, A♭4/G#4 = 416 Hz) and two of the tones were mistuned (1/4-semitone deviation of A♭4/G#4 = 422 Hz, 1/10-semitone deviation of A4 = 438 Hz). All piano tones were recorded as 16-bit stereo files and had a duration of 200 ms with 5-ms rise and fall time. Their overall amplitude was normalized to ensure equal intensities.

During EEG recording, the auditory stimuli were presented binaurally with HiFi headphones (Sennheiser, HD 25-1, 70 Ω, Ireland) at a sound pressure level of 70 dB. Stimulus presentation was controlled by the Presentation software (version 18.1, RRID:SCR_002521). The participants were instructed to watch a silent black and white film and to ignore the simultaneously presented auditory stimuli. This passive listening experiment consisted of five blocks, presented in a random order across participants. In each block, one of the five piano tones was presented more frequently (420 times, occurrence probability = 60%; standard tone) than the other four (70 times each, occurrence probability = 10%; deviant tones). Each piano tone served as standard tone in one block and as deviant tone in all other blocks. As the EEG analyses of the original study, we focused on the blocks with standard tones of 440 Hz (block A) and of 264 Hz (block C). In these blocks, deviation magnitude increased or decreased unambiguously. Therefore, it was possible to test the effect of deviation magnitude on the EEG signal. Table 2 provides an overview of the study design. Presentation of the stimuli was pseudorandomized in each block. To establish a stable memory trace (Näätänen and Winkler, 1999), the first 15 tones were standards. For the remaining trials, deviants were always followed by at least one standard tone, and at least two different deviants were inserted before the same deviant could appear again. The inter-

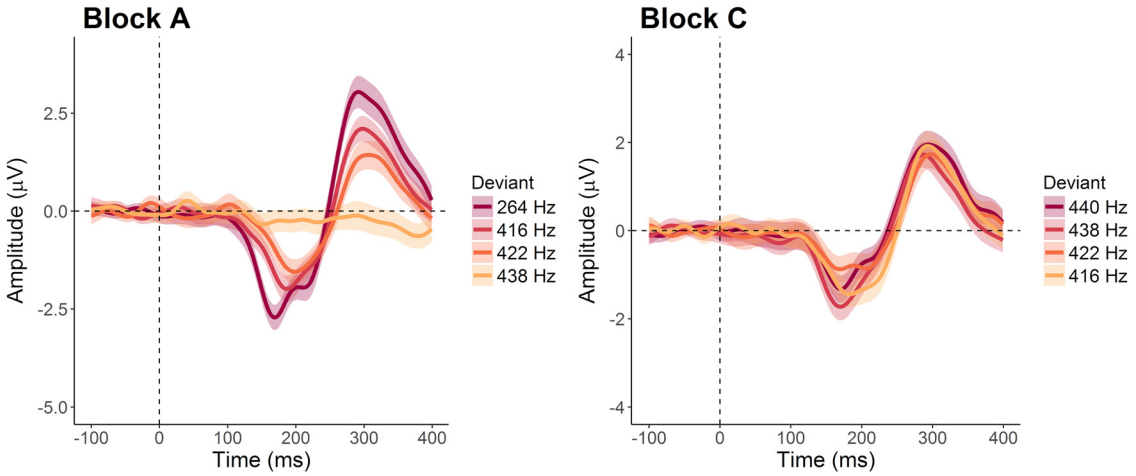

Figure 1. Grand averages of the difference waves (deviant ERP minus standard ERP). ERPs from the fronto-central pooling of electrodes were averaged over all participants for each deviation condition. The lines represent the means, the shaded areas indicate 95% within-subject confidence intervals. Darker colors illustrate larger deviation magnitudes. In block A (standard tone 440 Hz), amplitudes increase with larger deviation magnitude. In block C (standard tone 264 Hz), no such clear relationship can be observed.

stimulus interval between the tones was fixed to 550 ms. The entire EEG recording lasted around 45 min.

EEG recording and preprocessing

EEG data were recorded with a sampling rate of 1000 Hz and an online bandpass filter of 0.1–100 Hz using a BrainAmp amplifier (Brainproducts). Thirty-two silver/silver-chloride electrodes were placed according to a subset of the 10/10 system, and an electrode on the tip of the nose was used as the reference. Electrode impedance was kept below 10 kΩ by applying an electrically conductive gel.

Preprocessing of the EEG data was conducted with the BrainVision Analyzer software package (version 2.1, https://www.brainproducts.com/, RRID:SCR_002356). Data were filtered offline with a bandpass filter of 1–20 Hz (48 dB/octave) and a notch filter of 50 Hz. Eye movement artifacts (eye blinks and saccades) were corrected using an independent component analysis (ICA; Jung et al., 2000), and noisy channels were interpolated. Remaining artifacts were removed using an automatic raw data inspection algorithm when a voltage gradient criterion of 50 μV/ms, an amplitude criterion of ±100 μV, or a low activity criterion of 0.5 μV/100 ms was exceeded. After preprocessing, the EEG signal was divided into segments of 500 ms (–100–400 ms from stimulus onset). These segments were baseline corrected (–100–0 ms) and averaged to ERPs. To compute difference waves, the ERPs evoked by the five standard tones were subtracted from the ERPs evoked by the physically identical deviants presented in the two blocks of interest (block A and block C). The grand averages of the difference waves for each deviant over all participants are shown in Figure 1. In Figure 2, the grand averages are presented separately for each group.

We extracted peak values of the resulting difference waves for the MMN and P3a from a pooling of nine frontal and central electrodes (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4). In the original study, both ERP components elicited maximal amplitudes over these electrodes, and a similar voltage distribution could be observed in the data of the current replication study (Fig. 3; the topographical maps were created using code from the R package *EEGutils*; Craddock, 2018). Peaks were selected using an automatic peak detection algorithm and verified by visual inspections.

Statistical analyses

All statistical analyses were conducted in R (version 3.4.3; https://www.r-project.org, RRID:SCR_001905). To compare the groups in terms of demographics and musical experience, we applied Welch's *t* tests. Effect sizes for *t* tests are given in Cohen's *d* (Cohen, 1988).

For statistical analyses of the peak amplitudes and latencies, we replicated the null hypothesis statistical testing (NHST) of the original paper (replication analyses) and additionally performed Bayes factor analyses (exploratory Bayesian analyses).

In the replication analyses, a two-way mixed ANOVA with two levels of group (AP and non-AP) and four levels of deviation (four deviants) was computed separately for each ERP component and each block of interest using the R package *ez* (version 4.4.0; https://cran.r-project.org/web/packages/ez/index.html); *p* values and degrees of freedom were adjusted using Greenhouse–Geisser correction when Mauchly's test revealed non-sphericity. For the ANOVAs, generalized eta-squared (η^2_G) is reported as the effect size estimate (Bakeman, 2005). Additionally, we report Cohen's *d* for the main effect of group (Cohen, 1988). As in the original study, results with $p \leq 0.05$ are termed significant.

Bayes factors

Using NHST provides direct comparability with the original study. However, because NHST only allows to reject the null hypothesis (H0), but not the alternative

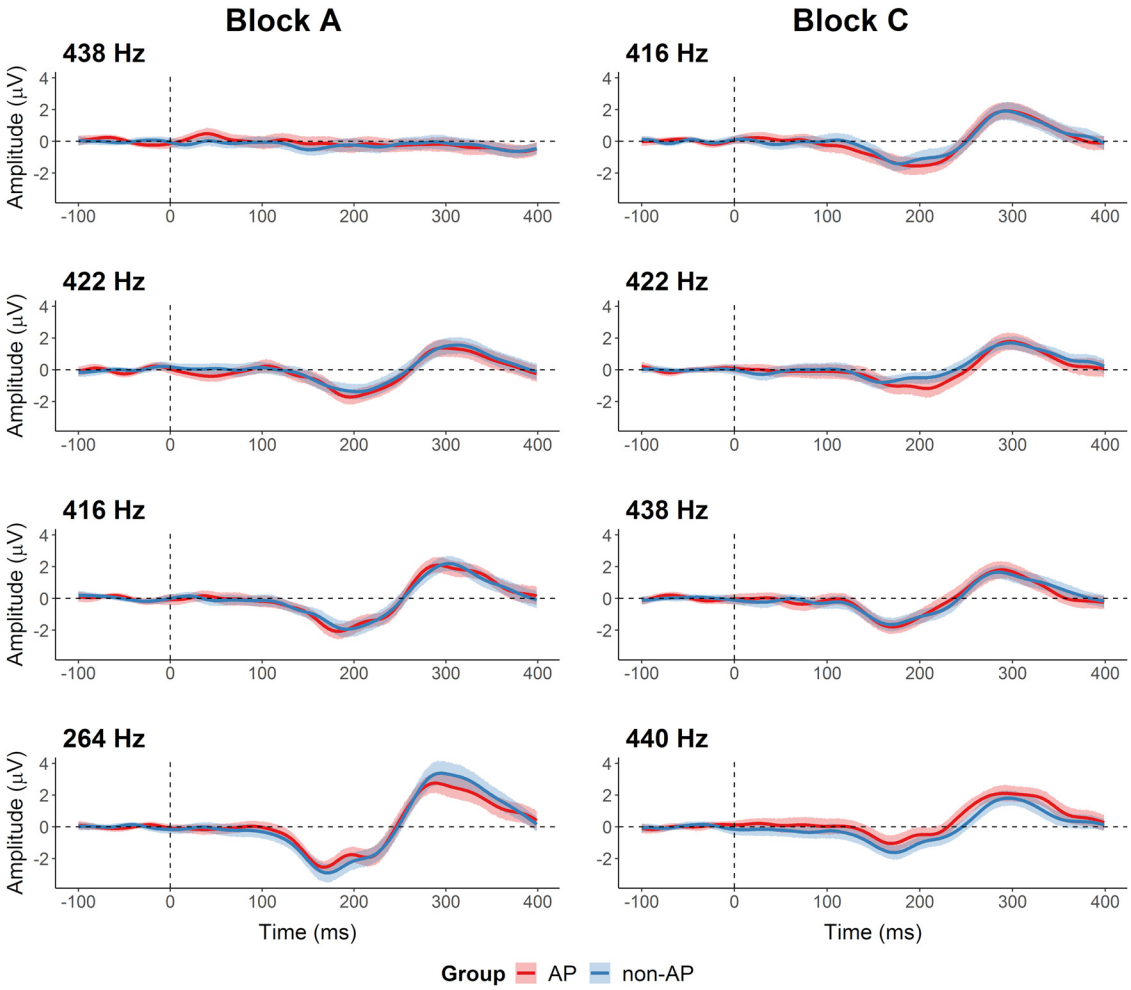

Figure 2. Grand averages of the difference waves (deviant minus standard) for AP (in red) and non-AP (in blue) musicians. Deviation magnitude increases from top to bottom. The lines represent the group means, the shaded areas represent the 95% between-subject confidence interval.

(H1), non-significant results cannot differentiate between insensitive data and evidence in favor of H0. To decide whether a replication was successful or not, a quantification of null results is especially useful. Contrary to NHST, Bayes factors allow such conclusions on whether the evidence supports H0, the evidence supports H1, or the evidence is ambiguous (Rouder et al., 2009; Dienes, 2011, 2014; Lee and Wagenmakers, 2013). Bayes factors express the ratio between the likelihood of the data under one hypothesis (e.g., H0) relative to another hypothesis (e.g., H1). A Bayes factor BF01 of 10 (or the inverse $1 / BF_{01} = BF_{10} = 0.1$) can be directly interpreted as the data being 10 times more likely to occur under H0 compared to H1. As a consequence, Bayes factors are well suited to interpret non-significant results (Dienes, 2014) and to quantify the success of a replication (Verhagen and Wagenmakers, 2014; Anderson and Maxwell, 2016).

We calculated Bayes factors using the default Cauchy priors (scaling factor $r = 0.707$) as implemented in the *BayesFactor* package in R (version 0.9.12-4.2; https://cran.r-project.org/web/packages/BayesFactor/index.html) with 100,000 iterations. Priors were not based on the effect sizes reported in the original study because small samples often result in inflated effect size estimates (Ioannidis, 2008; Button et al., 2013; Halsey et al., 2015). However, to ensure the robustness of our results, we additionally tested a range of priors (i.e., $r = 0.50$, $r = 1.00$, $r = 1.20$), and the results supported the same main conclusions.

Paralleling the replication analyses, we performed Bayesian ANOVAs (BANOVA; Rouder et al., 2017) on the peak amplitudes and latencies separately for each ERP component in each block. Bayes factors of interaction effects were assessed by comparing the full model (group + deviation + group × deviation + subject) to the model without the interaction effect (group + deviation + subject).

To facilitate interpretation, we report BF_{10} when Bayes factors favored the alternative hypothesis and BF_{01} ($1 / BF_{10}$) when Bayes factors favored the null hypothesis. Following Jeffreys (1961; edited by Lee and Wagenmakers, 2013)'s terminology, a Bayes factor between 1 and 3 is considered anecdotal evidence, between 3 and 10

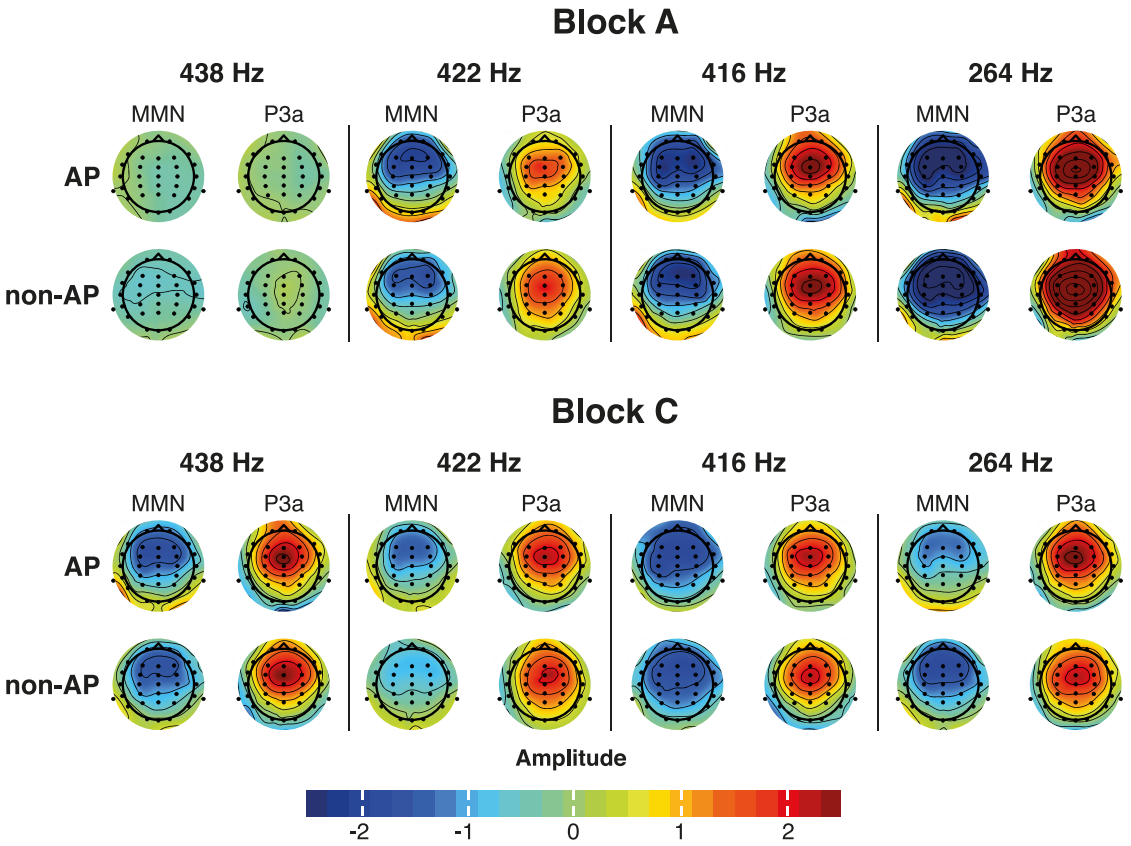

Figure 3. Voltage distributions over the scalp for the MMN and P3a for each group and each deviant in block A (standard tone 440 Hz) and block C (standard tone 264 Hz). Topographies are shown at the time point of the peak according to the grand average of the specific deviation condition and group. Deviation magnitude increases from left to right. Both MMN and P3a are maximally expressed at fronto-central electrode sites.

moderate evidence, between 10 and 30 strong evidence, between 30 and 100 very strong evidence, and above 100 extreme evidence for the respective hypothesis.

Results

Demographics and behavioral data

Welch's *t* tests did not reveal any significant group differences in age ($t_{(100.58)} = 1.39$, $p = 0.17$, $d = 0.27$), intelligence ($t_{(101.99)} = -1.43$, $p = 0.15$, $d = 0.28$), age of onset of musical training ($t_{(100.89)} = -1.16$, $p = 0.25$, $d = 0.23$), and cumulative musical training hours over the lifespan ($t_{(99.49)} = 1.41$, $p = 0.16$, $d = 0.27$). However, the two groups differed in musical aptitude ($t_{(99.41)} = 2.23$, $p = 0.028$, $d = 0.44$), and AP musicians performed significantly better in the pitch-labeling test ($t_{(101.75)} = 13.77$, $p < 0.001$, $d = 2.70$; Fig. 4).

Electrophysiological data: replication analyses

The analyses of the MMN amplitudes and latencies showed similar results as in the original study. The original study reported main effects of deviation for MMN amplitudes and latencies, but only in block A. In the present study, we found a significant main effect of deviation on MMN amplitudes in both block A ($F_{(2.90,296.15)} = 45.60$, $p < 0.001$, $\eta^2_G = 0.21$) and block C ($F_{(2.92,297.71)} = 4.28$, $p = 0.006$, $\eta^2_G = 0.03$). However, the generalized eta-squared indicated that the effect in block C was small and comparable to the one obtained in the original study ($\eta^2_G = 0.04$). Additionally, as visible in Figures 1, 5, the amplitudes did not consistently get larger with increasing deviation magnitude in block C. As in the original study, the analysis did not reveal any significant effects of group (block A: $F_{(1,102)} = 0.45$, $p = 0.51$, $\eta^2_G = 0.002$, $d = 0.08$; block C: $F_{(1,102)} = 1.52$, $p = 0.22$, $\eta^2_G = 0.005$, $d = 0.14$) or significant interactions for MMN amplitudes (block A: $F_{(2.90,296.15)} = 0.52$, $p = 0.66$, $\eta^2_G = 0.003$; block C: $F_{(2.92,297.71)} = 1.87$, $p = 0.14$, $\eta^2_G = 0.01$).

A similar pattern was found for MMN latencies. There was a significant main effect of deviation in block A ($F_{(2.52,256.66)} = 4.99$, $p = 0.004$, $\eta^2_G = 0.03$) and block C ($F_{(2.86,291.60)} = 7.60$, $p < 0.001$, $\eta^2_G = 0.04$), but effect sizes were small. The main effects of group (block A: $F_{(1,102)} = 0.01$, $p = 0.94$, $\eta^2_G < 0.001$, $d = 0.008$; block C: $F_{(1,102)} = 0.42$, $p = 0.52$, $\eta^2_G = 0.002$, $d = 0.08$) and the interactions (block A: $F_{(2.52,256.66)} = 0.78$, $p = 0.48$, $\eta^2_G = 0.005$; block C: $F_{(2.86,291.60)} = 0.80$, $p = 0.49$, $\eta^2_G = 0.004$) did not reach significance.

The main result reported in the original study were reduced P3a amplitudes in AP musicians compared to non-AP musicians. P3a latencies were not evaluated in the original study but are reported here for completeness. In line with the original study, the replication analyses

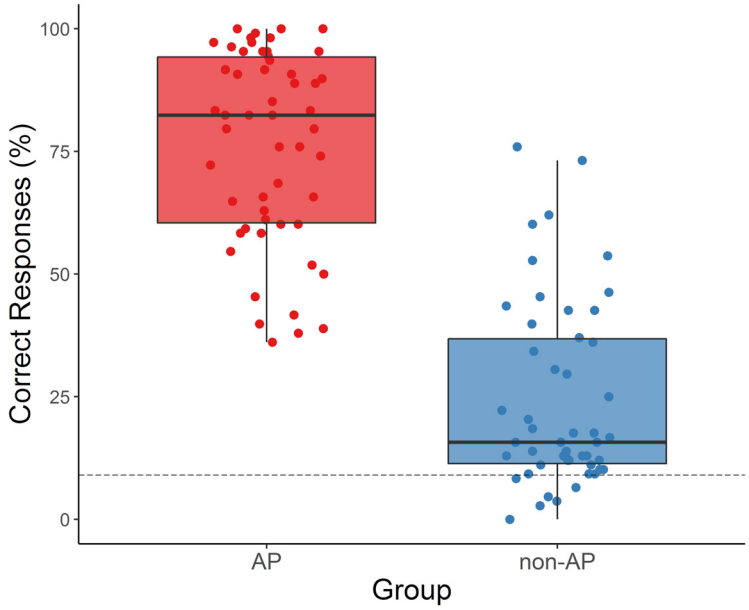

Figure 4. Performance in the pitch-labeling test for AP and non-AP musicians. Octave errors were treated as correct answers, resulting in a chance level of 8.33% (dashed line). AP musicians are depicted in red, non-AP musicians in blue. AP musicians performed significantly better than non-AP musicians ($t_{(101.75)} = 13.77$, $p < 0.001$, $d = 2.70$).

showed a significant main effect of deviation on P3a amplitudes in block A ($F_{(2.63,268.46)} = 55.02$, $p < 0.001$, $\eta^2_G = 0.25$), but not in block C ($F_{(2.87,292.91)} = 1.39$, $p = 0.25$, $\eta^2_G = 0.007$). However, contrary to the original study, we did not find any significant main effects of group (block A: $F_{(1,102)} = 0.08$, $p = 0.78$, $\eta^2_G = 0.002$, $d = 0.03$; block C: $F_{(1,102)} = 1.19$, $p = 0.28$, $\eta^2_G = 0.006$, $d = 0.15$) or interaction effects (block A: $F_{(2.63,268.46)} = 0.92$, $p = 0.42$, $\eta^2_G = 0.005$; block C: $F_{(2.87,292.91)} = 1.14$, $p = 0.33$, $\eta^2_G = 0.005$) for P3a amplitudes (Fig. 5).

The analysis of P3a latencies also revealed a significant main effect of deviation in block A ($F_{(2.22,226.56)} = 5.58$, $p = 0.003$, $\eta^2_G = 0.04$), but no significant main effect of group ($F_{(1,102)} = 0.09$, $p = 0.77$, $\eta^2_G < 0.001$, $d = 0.03$) and no interaction ($F_{(2.22,226.56)} = 0.50$, $p = 0.63$, $\eta^2_G = 0.003$). In block C, there was no significant main effect (deviation: $F_{(2.87,292.44)} = 1.58$, $p = 0.20$, $\eta^2_G = 0.009$; group: $F_{(1,102)} = 0.05$, $p = 0.82$, $\eta^2_G < 0.001$, $d = 0.03$) or interaction ($F_{(2.87,292.44)} = 0.43$, $p = 0.72$, $\eta^2_G = 0.002$).

Electrophysiological data: exploratory Bayesian analyses

Replication analyses of MMN and P3a amplitudes yielded non-significant results for all group comparisons. To better distinguish between insensitive evidence, evidence for the alternative hypothesis, and evidence for the null hypothesis, we computed Bayes factors.

For MMN amplitudes, the Bayes factors mostly mirrored the results from the replication analyses. In block A, we obtained extreme evidence for an effect of deviation ($BF_{10} = 7.32 \times 10^{21}$), moderate evidence for the absence of an effect of group ($BF_{01} = 5.93$) and strong evidence for the absence of an interaction effect ($BF_{01} = 21.52$). In block C, evidence for an effect of deviation was less strong than in block A ($BF_{10} = 3.25$). Further, Bayes factors showed moderate evidence that there was no group difference ($BF_{01} = 3.70$) and no interaction ($BF_{01} = 3.92$).

As in the replication analyses, results for the MMN latencies were similar to those obtained for MMN amplitudes. Bayes factors provided evidence for the existence of a difference between deviants in block A ($BF_{10} = 9.36$) and block C ($BF_{10} = 242.91$), but not for differences between groups (block A: $BF_{01} = 7.17$; block C: $BF_{01} = 5.10$) or for an effect of interaction (block A: $BF_{01} = 15.28$; block C: $BF_{01} = 15.77$).

The replication analyses of P3a amplitudes revealed a significant effect of deviation in block A. All other effects did not reach significance. Bayes factors strongly supported the existence of a difference between deviants in block A ($BF_{10} = 2.06 \times 10^{26}$), but not in block C ($BF_{01} = 15.86$). In terms of group differences, there was moderate evidence for the null hypothesis in both block A ($BF_{01} = 7.32$) and block C ($BF_{01} = 3.14$). Bayes factors also strongly favored the null hypothesis regarding the interaction (block A: $BF_{01} = 13.40$; block C: $BF_{01} = 10.40$).

For P3a latencies, there was strong evidence for an effect of deviation in block A ($BF_{10} = 26.64$). For all other effects, Bayes factors provided support for the null hypothesis in both block A (group: $BF_{01} = 7.29$; interaction: $BF_{01} = 22.07$) and block C (deviation: $BF_{01} = 15.86$; group: $BF_{01} = 6.30$; interaction: $BF_{01} = 10.40$).

Electrophysiological data: exploratory subgroup analyses

The sample of the present study differed from the sample of the original study in three main ways: First, our sample was quite evenly balanced in terms of gender while the original study investigated predominantly female subjects. This might have influenced the results as fe-

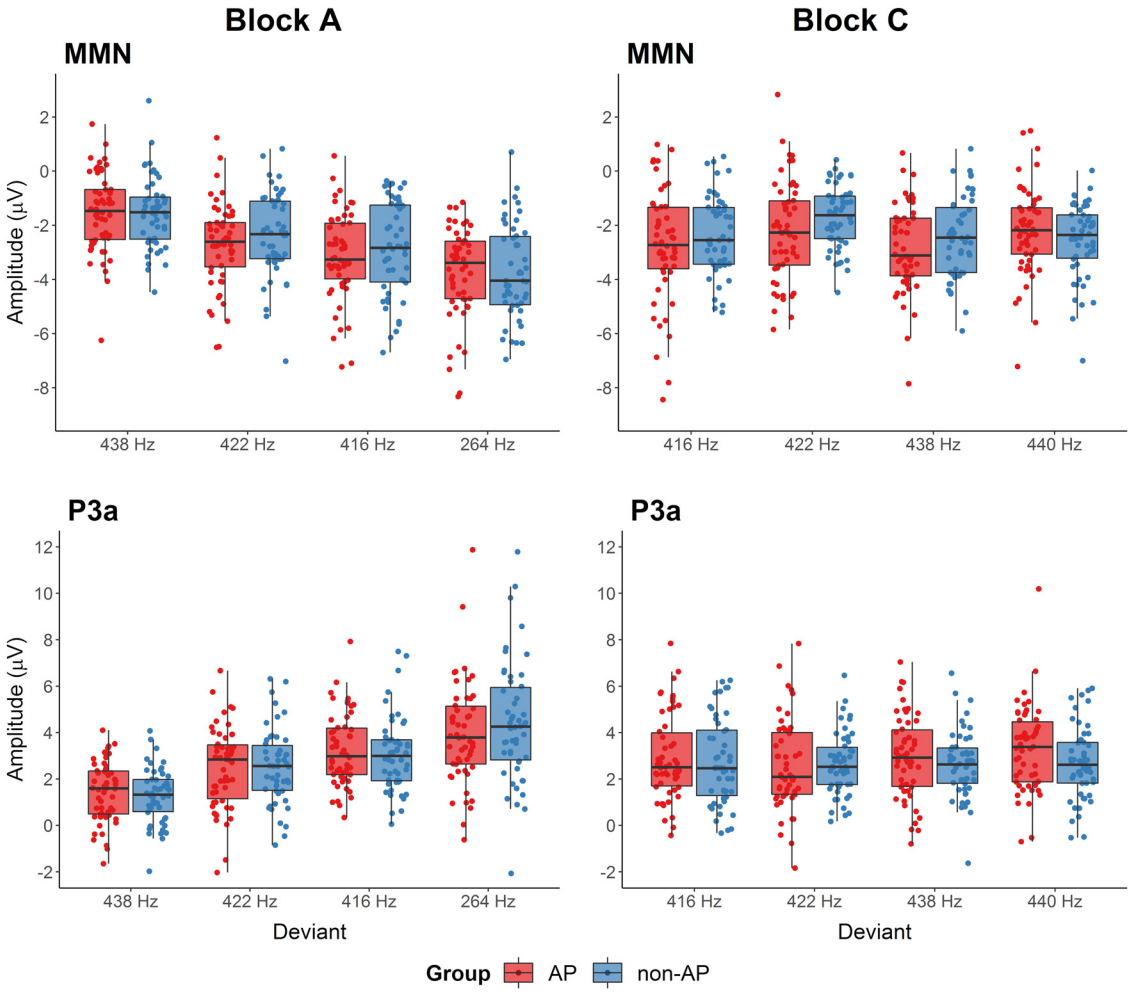

Figure 5. MMN and P3a amplitudes of musicians with AP and without AP (non-AP) for all deviation conditions in block A (standard tone 440 Hz) and block C (standard tone 264 Hz). Deviants are ordered from left to right according to increasing deviation magnitude. Amplitudes of AP musicians are shown in red, amplitudes of non-AP musicians are shown in blue.

males have previously been shown to have larger P3a amplitudes than males (visual paradigm, Conroy and Polich, 2007). Second, there was no overlap between the two groups in the pitch-labeling scores in the original study, but there is an overlap in our sample. Third, there was a small but significant difference in musical aptitude (AMMA) between groups in the present study.

Since all these sample differences could account for the differences in the results, we conducted additional subgroup analyses for the P3a amplitude. One subgroup analysis was performed on just the female participants of our study ($n_{AP} = 27$, $n_{non\text{-}AP} = 24$). A second subgroup analysis was performed on the third of the participants with the lowest pitch-labeling scores (<31.79%, $n = 35$) and the third of the participants with the highest pitch-labeling scores (>72.83%, $n = 35$). This allowed us to check whether the absence of the AP effect on the P3a was due to the more heterogenous groups in the present study. A third subgroup analysis corresponded as closely as possible to the original study in terms of pitch-labeling scores and sample size: only participants with scores <10% ($n = 9$) and >93% ($n = 15$) entered this analysis. Finally, we also performed an analysis of covariance (ANCOVA) with the AMMA score as covariate to test whether the between-group difference in musical aptitude influenced the result.

For the subgroup of females only, analysis of the P3a amplitude revealed an effect of deviation in block A ($F_{(2.75,134.94)} = 21.83$, $p < 0.001$, $\eta^2_G = 0.23$, $BF_{10} = 1.13 \times 10^{10}$) but no effect of group ($F_{(1,49)} = 0.20$, $p = 0.66$, $\eta^2_G = 0.001$, $d = 0.063$, $BF_{01} = 4.95$) or an interaction effect ($F_{(2.75,134.94)} = 0.35$, $p = 0.77$, $\eta^2_G = 0.004$, $BF_{01} = 12.72$). No significant effect was found in block C (group: $F_{(1,49)} = 0.29$, $p = 0.59$, $\eta^2_G = 0.003$, $d = 0.11$, $BF_{01} = 3.43$; deviation: $F_{(2.89,141.73)} = 0.68$, $p = 0.56$, $\eta^2_G = 0.007$, $BF_{01} = 17.61$; interaction: $F_{(2.89,141.73)} = 0.35$, $p = 0.78$, $\eta^2_G = 0.003$, $BF_{01} = 12.74$).

Similarly, the analysis with the lowest and highest performing third of participants showed an effect of deviation in block A ($F_{(2.63,178.59)} = 38.39$, $p < 0.001$, $\eta^2_G = 0.27$, $BF_{10} = 9.96 \times 10^{17}$) but no effect of group ($F_{(1,68)} = 0.04$, $p = 0.83$, $\eta^2_G < 0.001$, $d = 0.09$, $BF_{01} = 5.18$) or an interaction effect ($F_{(2.63,178.59)} = 0.38$, $p = 0.74$, $\eta^2_G = 0.003$, $BF_{01} = 18.79$). Again no significant effects were observed in block C (group: $F_{(1,68)} = 2.72$, $p = 0.11$, η^2_G

= 0.02, d = 0.35, BF_{10} = 1.50; deviation: $F_{(2.78,188.84)}$ = 0.93, p = 0.42, η^2_G = 0.007, BF_{01} = 18.74; interaction: $F_{(2.78,188.84)}$ = 2.42, p = 0.072, η^2_G = 0.02, BF_{01} = 2.88).

Likewise, with even more extreme groups (<10% and >93% pitch-labeling performance), there was an effect of deviation in block A ($F_{(2.54,55.91)}$ = 24.34, p < 0.001, η^2_G = 0.44, BF_{10} = 5.97 × 10^9) but no other effect in block A (group: $F_{(1,22)}$ = 0.03, p = 0.86, η^2_G < 0.001, d = 0.03, BF_{01} = 3.62; interaction: $F_{(2.54,55.91)}$ = 0.64, p = 0.57, η^2_G = 0.02, BF_{01} = 4.61) or block C (group: $F_{(1,22)}$ = 2.68, p = 0.12, η^2_G = 0.06, d = 0.55, BF_{01} = 1.03; deviation: $F_{(2.67,58.74)}$ = 1.22, p = 0.31, η^2_G = 0.02, BF_{01} = 4.61; interaction: $F_{(2.67,58.74)}$ = 0.91, p = 0.43, η^2_G = 0.02, BF_{01} = 2.94).

The ANCOVA with the AMMA score as covariate on the full sample revealed similar results: an effect of deviation in block A ($F_{(2.63,268.46)}$ = 55.02, p < 0.001, η^2_G = 0.25) and no other effects neither in block A (group: $F_{(1,102)}$ = 0.04, p = 0.85, η^2_G < 0.001; interaction: $F_{(2.63,268.46)}$ = 0.92, p = 0.42, η^2_G = 0.01) nor in block C (group: $F_{(1,102)}$ = 1.95, p = 0.17, η^2_G = 0.009; deviation: $F_{(2.87,292.91)}$ = 1.39, p = 0.25, η^2_G = 0.007; interaction: $F_{(2.87,292.91)}$ = 1.14, p = 0.33, η^2_G = 0.006).

We also performed an ANCOVA on the subgroup of participants with comparable sample size and pitch-labeling scores as in the original study. Again, we found an effect of deviation in block A ($F_{(2.54,55.91)}$ = 24.34, p < 0.001, η^2_G = 0.44) but no other effects in either block A (group: $F_{(1,22)}$ = 0.04, p = 0.85, η^2_G < 0.001; interaction: $F_{(2.54,55.91)}$ = 0.64, p = 0.57, η^2_G = 0.02) or block C (group: $F_{(1,22)}$ = 3.81, p = 0.064, η^2_G = 0.08; deviation: $F_{(2.67,58.74)}$ = 1.22, p = 0.31, η^2_G = 0.03; interaction: $F_{(2.67,58.74)}$ = 0.91, p = 0.43, η^2_G = 0.02).

Discussion

In the present study, we attempted to replicate Rogenmoser et al. (2015)'s finding of electrophysiological group differences between AP and non-AP musicians during passive listening. Rogenmoser et al. (2015) investigated the automatic nature of AP by recording EEG during a passive auditory oddball paradigm. By analyzing MMN and P3a, they intended to assess the contribution of both pre-attentive (as reflected by the MMN) and more cognitive processes (as reflected by the P3a) in AP. To compare the tone processing between AP and non-AP musicians under different deviation conditions, they applied a paradigm with multiple tuned and mistuned deviants. In line with previous research (Tervaniemi et al., 1993; Matsuda et al., 2013, condition with tuned tones), they did not find any significant group differences in the MMN. In contrast, Rogenmoser et al. (2015) observed smaller P3a amplitudes in AP musicians. This group difference was only found in conditions in which the deviation magnitude was larger than one semitone (264-Hz deviant in block A and all deviants in block C), suggesting that AP musicians process between-pitch but not within-pitch categories differentially than non-AP musicians. Because the P3a has been associated with an early reallocation of attention (Escera et al., 1998; Friedman et al., 2001; Kujala et al., 2007; Polich, 2007), the smaller amplitudes in AP musicians were interpreted as an indication for more efficient cognitive tone processing in AP. The authors concluded that the "P3a component turned out to be a specific marker for AP" (Rogenmoser et al., 2015).

In the current direct replication study, we found no significant group differences in the MMN, confirming the results of the original study. However, and most critically, there were also no significant group differences in the P3a. Additional Bayes factor analyses revealed that the data are more likely under the null hypothesis, implying that AP and non-AP musicians' tone processing, as indicated by MMN and P3a peak amplitudes and latencies, does not differ during passive listening. Thus, our results challenge the view of cognitive facilitation in AP during passive listening.

In passive auditory oddball paradigms, the MMN typically occurs in response to a change (deviation) in auditory stimulation within a sequence of repeated stimuli (standard tone). The main generator of the MMN is located in the auditory cortex (for review, see Näätänen et al., 2007), where the repeated presentation of a stimulus potentially causes the formation of a short-term memory trace (Näätänen and Winkler, 1999). The MMN is generated when a new auditory input differs from the representation in this sensory memory trace. Because this mismatch detection process does not require that the stimuli are attended, it is thought to be automatic (Sussman et al., 2003; Paavilainen et al., 2007). Accordingly, the MMN is considered an objective measure of auditory discrimination accuracy (Näätänen et al., 2007). Consistent with this view, it has been shown that the amplitude of the MMN increases when discrimination performance improves through training (Näätänen et al., 1993; Menning et al., 2000; Atienza et al., 2002). The MMN amplitude also correlates more generally with behavioral discrimination accuracy (Novak et al., 1990; Näätänen et al., 1993). Similarly, the MMN is also influenced by the deviation magnitude, with larger, and therefore more salient, deviations evoking larger amplitudes and shorter latencies (Sams et al., 1985; Berti et al., 2004; Novitski et al., 2004).

The original study reported an effect of deviation magnitude for block A but not for block C. The authors provided a possible explanation that in block C, all deviants were clustered around an extreme deviation level, with a distance between eight and nine semitones from the standard tone. Consequently, all deviants were probably equally easy to detect. In accordance with the original study, our results showed larger MMN amplitudes and shorter MMN latencies for larger deviations in block A. In block C, the effect also reached significance, but like in the original study, amplitudes did not unambiguously increase with deviation magnitude (compare Fig. 3), suggesting a context effect in this specific block.

More importantly, we also replicated the result of non-significant group differences between the AP and non-AP musicians in MMN measures. The Bayes factor analysis additionally provided support for the null hypothesis. Thus, our data were more likely under the hypothesis that there were no differences in the MMN amplitudes and latencies between the two groups than under the H_1. Our

results are not only consistent with the original study but also with other previous research. Using tuned and mistuned pure tones and piano tones, Tervaniemi et al. (1993) did not find group differences between AP and non-AP musicians in MMN amplitudes and latencies. In Matsuda et al. (2013)'s study, MMN amplitudes of AP and non-AP musicians did also not differ for tuned tones, but AP musicians showed larger MMN amplitudes for mistuned tones. However, this effect might have been influenced by the fact that their AP musicians were musically more experienced than the non-AP musicians. Previous research has shown that musical experience can increase MMN amplitudes (Koelsch et al., 1999; Putkinen et al., 2014), specifically in response to mistuned tones (Tervaniemi et al., 2014).

Because the MMN is associated with a passive discrimination process, Tervaniemi et al. (1993) concluded from their results that "pitch naming and discrimination are based on different brain mechanisms." This coincides with results from behavioral studies showing that pitch-labeling accuracy is not correlated with behavioral pitch-discrimination accuracy (Sergeant, 1969; Fujisaki and Kashino, 2002). Thus, evidence from both behavioral and electrophysiological data suggests that AP does not simply rely on refined pitch discrimination.

In passive auditory oddball paradigms, the MMN is often followed by the P3a, a subcomponent of the P300. Both components have been proposed to play a role in the reallocation of attention to unattended stimuli (Näätänen, 1990; Escera et al., 2000; Kujala et al., 2007), with the processes underlying MMN probably initiating the attention switching and the P3a directly reflecting it. The P3a is affected by the magnitude of deviation in similar ways as the MMN (Berti et al., 2004). As for the MMN, the original study found such a deviation modulation only in block A, probably again due to the more extreme deviation levels in block C. The present study successfully replicated these results. In block A, P3a amplitudes increased and P3a latencies decreased with increasing deviation, and as in the original study, no similar effect was observed in block C. Future studies should more systematically investigate this dependence on specific contexts.

Although the modulation of the MMN and P3a as a function of deviation magnitude is an interesting aspect of general pitch processing, the main finding of the original study was the reduced P3a amplitudes in AP musicians. This result was compared to findings from the parietal P3b, another subcomponent of the P300, which is elicited in active oddball paradigms and often called P300 in these studies. The P3b has been linked to working memory updating (for review, see Kok, 2001; Polich, 2007) and has been investigated more thoroughly in AP research than the P3a. The first study to detect differences in ERPs during pitch processing reported the absence of a P3b in individuals with AP (Klein et al., 1984). This was regarded as an indication that individuals with AP did not need to update their auditory working memory during the task because their pitch representations are permanent. Subsequently, some studies replicated the absence or diminution of P3b amplitudes in AP (Hantz et al., 1992; Wayman et al., 1992; Crummer et al., 1994), but others did not (Hantz et al., 1995; Hirose et al., 2002). . This inconsistency was shown to be caused by differential pitch-processing strategies (RP or AP) employed by the participants based on the specific task instructions, the task difficulty, and the individual level of AP (Bischoff Renninger et al., 2003).

Individual differences in listening strategies could explain why we did not replicate the effect of AP on the P3a. However, this seems rather unlikely as the use of top-down strategies was controlled with the help of a distractor task (watching a silent film) in both the original and the replication study. Given how unreliable the effect of AP on ERPs is even in active tasks, we believe it is more plausible that the differences in passive pitch processing are too subtle to be reliably detectable with ERP peak measures. Alternatively, it could also be speculated that the pitch labeling is only initiated when actively attending the auditory stimuli or when performing a labeling-related task (e.g., bimodal Stroop task; Akiva-Kabiri and Henik, 2012). Compelling evidence for an automatic pitch-labeling process comes from behavioral studies, in which the auditory stimuli had to be attended to solve the task. For instance, individuals with AP performed poorer in auditory Stroop tasks when they heard sung tone names and were instructed to repeat the syllable while ignoring the pitch it was sung in (Miyazaki, 2004; Itoh et al., 2005; Schulze et al., 2013). AP also hindered performance in a RP task, in which participants had to compare a visual notation with the auditory presentation of a melody (Miyazaki and Rakowski, 2002). Further evidence for the automaticity of pitch labeling was provided by neuroscientific studies that observed differential electrophysiological or hemodynamic responses in AP musicians during attentive listening (Zatorre et al., 1998; Itoh et al., 2005). Contrary to these studies, in the present study, participants were instructed to focus their attention on a silent film and to ignore the auditory stimuli altogether. AP musicians can label tones fast and effortlessly, but they may not necessarily do so under all circumstances. Apart from the specific task, also other situational factors like stress and fatigue might influence pitch-labeling performance and pitch-labeling automaticity. Additionally, it is also possible that there are considerable interindividual differences in the level of automaticity of AP per se. Future studies will hopefully uncover the role of such influences on this extraordinary ability and its neural underpinnings in more detail.

Although this study could not demonstrate a cognitive facilitation in AP during passive listening, we believe our results do not challenge existing cognitive theories of AP, like the two-component model (Levitin, 1994). The two-component model focuses on the use of long-term pitch memory representations and their association with labels in AP. This mechanism in turn poses less demands on working memory in some tasks than using RP (Klein et al., 1984; Itoh et al., 2005; Schulze et al., 2009). In contrast to these mnemonic processes, the P3a in passive auditory oddball paradigms is mostly associated with attentional

processes, which are not explicitly postulated as part of AP by the two-component model. Further research should be undertaken to determine the influence of attention on pitch processing in AP.

We attempted a direct replication of the original study, still there are some mentionable differences between the original and the replication study that might have influenced the results. While questionnaires on musical experience and the pitch-labeling test were assessed with paper-pencil in the original study, we used online questionnaires and an online pitch-labeling test in the present study. Because our participants underwent an extensive test protocol in the context of the larger AP project spanning several days during which they participated in various (f)MRI and EEG experiments, we tried to keep the travel burden for them as low as possible by providing the opportunity to work on several tests at home. For our statistical analyses, we used the software R instead of SPSS, and we performed Welch's *t* tests instead of Student's *t* test because they are more robust for groups with unequal sample sizes (Ruxton, 2006; Delacre et al., 2017). For ANOVAs, we reported generalized eta-squared instead of partial eta-squared as recommended by Bakeman (2005). Like in the original study, groups were defined based on self-report. Contrary to the original study, in our replication study, the non-AP musicians performed above chance in the pitch-labeling test. Accordingly, it could be argued that the groups were less homogenous than in the original study and that this is the reason for the unsuccessful replication. However, because trials in the pitch-labeling test lasted 15 s instead of 5 s, participants probably had enough time to employ RP strategies in our test. It can be expected that highly-trained musicians perform above chance levels when given the opportunity to use RP strategies. For the same reason, it is possible that the pitch-labeling performance of AP musicians was also overestimated. The longer maximal trial duration was due to the online implementation of the pitch-labeling test. In a pilot study, we tested a version with the original trial duration of 5 s, which turned out to be very demanding and difficult to solve even for AP musicians because of the multiple-choice format with 36 answer options. We would recommend future studies to measure reaction times in pitch-labeling tests to be able to better disentangle the effortless and fast AP strategy from the slower RP strategy, or to apply a pitch-labeling test that impedes the usage of RP strategies (e.g., as suggested in Wengenroth et al., 2014). Yet, it still remains unclear which is the best way to objectively identify AP ability and if it is even possible to do so, a question that has been asked frequently and was also discussed in an early influential review on AP (Takeuchi and Hulse, 1993). The authors addressed several methods to quantify AP, ranging from producing tones to different variants of pitch-labeling tests. Up to date, the pitch-labeling tests applied in AP research differ considerably in procedure (e.g., trial duration, answer registration, sine tones/instrumental tones), the number of used tones, and the presentation technique (e.g., online vs lab). Most importantly, no specific cutoff has been established to distinguish AP from non-AP possessors. Thus, in the present study, the pitch-labeling test only served as a validation tool. For group assignment, we relied on self-report since only the participants themselves can judge whether they possess the ability to employ AP strategies. In addition, as demonstrated in the exploratory subgroup analyses, the conclusions of the results remained the same even when just considering participants with the lowest and highest pitch-labeling scores, suggesting that this sample difference between studies did not cause the absence of the AP effect. Similarly, conclusions about the P3a amplitude did not change when just looking at the female participants. Thus, although the original study was less balanced in terms of gender than the present study, the absence of an effect of AP on the P3a amplitude in the present study does not seem to be caused by gender distribution differences between studies. Also, according to current scientific understanding gender differences in neuroscientific cognitive studies are most often due to small sample sizes and should only be interpreted when the influence of hormonal levels was controlled for (Jäncke, 2018). It should also be mentioned that in the present study, the AP and non-AP musicians showed a statistically significant, albeit small in absolute terms (less than three points out of 80 possible points), difference in musical aptitude (AMMA). However, scores are comparable to those reported in the original study, and additional covariance analyses with the AMMA score as covariate showed the same results as the replication analyses.

Finally, it is important to note that a single replication study can never conclusively confirm or disconfirm previous findings. Nevertheless, our results cast reasonable doubt that there is cognitive facilitation in AP during passive tone processing as indicated by the P3a. The more so since our sample was four times the size of the original study, and Bayes factors analyses provided evidence that the proposed effect does not exist. Although it is possible that additional factors we did not control for moderated the effect, we reduced such moderators to a minimum by doing a direct replication. Thus, if an effect of AP on the P3a really exists, its true effect size is probably much smaller than reported in the original study as it is not reliably detectable in a large sample, and its generalizability might be limited.

Considering the large effect size obtained in the original study, the results of the current study demonstrate that only through replications a better estimate of the true effect can be obtained. We believe replications are desirable in science in general and particularly in research fields that are prone to false-positive results and to overestimations of effect sizes due to small samples. Neuroscientific studies often use small samples because of the high financial costs and time-consuming data acquisition and analysis. Collaborative efforts between multiple research groups are suggested as a means to recruit larger sample sizes.

In summary, our direct replication of Rogenmoser et al. (2015) successfully replicated the non-significant results for group differences in the MMN. In contrast, we did not replicate the finding of smaller P3a amplitudes in AP

musicians. Taken together, our study does not support electrophysiological differences between AP and non-AP musicians during passive listening. It is conceivable that the different pitch-processing modes of AP and RP can only be reliably distinguished either with more sensitive measures or in more attention-engaging tasks. In more general terms, the results of the present study underline both the importance of replications and of larger sample sizes in neuroscientific research.

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Chapter 3 Empirical Work: Article 2

Heterogeneity of EEG resting-state brain networks in absolute pitch

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Abstract

The neural basis of absolute pitch (AP), the ability to effortlessly identify a musical tone without an external reference, is poorly understood. One of the key questions is whether perceptual or cognitive processes underlie the phenomenon, as both sensory and higher-order brain regions have been associated with AP. To integrate the perceptual and cognitive views on AP, here, we investigated joint contributions of sensory and higher-order brain regions to AP resting-state networks.

We performed a comprehensive functional network analysis of source-level EEG in a large sample of AP musicians (n = 54) and non-AP musicians (n = 51), adopting two analysis approaches: First, we applied an ROI-based analysis to examine the connectivity between the auditory cortex and the dorsolateral prefrontal cortex (DLPFC) using several established functional connectivity measures. This analysis is a replication of a previous study which reported increased connectivity between these two regions in AP musicians. Second, we performed a whole-brain network-based analysis on the same functional connectivity measures to gain a more complete picture of the brain regions involved in a possibly large-scale network supporting AP ability.

In our sample, the ROI-based analysis did not provide evidence for an AP-specific connectivity increase between the auditory cortex and the DLPFC. The whole-brain analysis revealed three networks with increased connectivity in AP musicians comprising nodes in frontal, temporal, subcortical, and occipital areas. Commonalities of the networks were found in both sensory and higher-order brain regions of the perisylvian area. Further research will be needed to confirm these exploratory results.

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Heterogeneity of EEG resting-state brain networks in absolute pitch

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ABSTRACT

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1. Introduction

Absolute pitch (AP) is the rare ability to effortlessly identify the pitch of a musical tone without the aid of an external reference tone (Deutsch, 2013). The neural mechanisms underlying AP are poorly understood. One central issue concerns the question of to what extent perceptual and cognitive processes contribute to the phenomenon. On the one hand, evidence from both structural and functional neuroimaging points towards an involvement of auditory regions (Keenan et al., 2001; McKetton et al., 2019; Schlaug et al., 1995), supporting the view of altered perceptual processing in AP (Kim and Knösche, 2017a). On the other hand, the two-component model, a prominent cognitive theory of AP, postulates that the association of long-term pitch representations with their labels (pitch labeling) constitutes the neurophysiological fundament of AP (Levitin, 1994). This pitch-labeling process has been associated with neural activation in the dorsolateral prefrontal cortex (DLPFC) (Bermudez and Zatorre, 2005; Zatorre et al., 1998).

Aiming to integrate the perceptual and cognitive perspectives on AP, the current study examined EEG resting-state connectivity for contributions of both sensory and higher-order brain regions to AP networks. Electroencephalographic resting-state activity has repeatedly been demonstrated to contain stable individual-specific information (e.g., Näpflin et al., 2007; Paranjape et al., 2001; Poulos et al., 2002; Valizadeh et al., 2019). Additionally, it has been shown that music-specific networks can be observed during resting state: Professional musicians exhibit increased EEG resting-state connectivity between brain regions that are involved in music processing and music production (Klein et al., 2015). Resting-state connectivity patterns in AP musicians might similarly reflect a network of brain regions underlying this specific expertise.

Analyzing resting-state EEG, a previous study of our group (Elmer et al., 2015) found some evidence that the auditory cortex and the DLPFC in the left hemisphere were functionally more strongly connected in AP musicians than in non-AP musicians. However, the study focused solely on these two regions of interest (ROIs) within each

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hemisphere. While this ROI-based approach minimizes the multiple comparisons problem, it neglects the possibility that the two ROIs could be part of a more extensive network. According to current scientific knowledge, various cognitive functions rely on interactions between distributed brain regions organized within large-scale networks (Bressler and Menon, 2010; Fuster, 2006; Petersen and Sporns, 2015; Sporns et al., 2004). The same might apply to AP. Findings from fMRI resting-state studies are in line with a more widespread resting-state network in AP musicians. A graph-theoretical study revealed increased clustering, degrees, strength, and local efficiency during rest in AP musicians not only in the superior temporal gyrus but also on a whole-brain level (Loui et al., 2012). Another fMRI study reported increased resting-state connectivity between the right planum polare and the auditory cortex (Kim and Knösche, 2017b). More recently, Brauchli et al. (2019a) identified increased local resting-state functional connectivity in the left anterior middle frontal gyrus (in the vicinity of the DLPFC) and in the left intraparietal sulcus, and increased global resting-state functional connectivity in the right superior parietal lobule. This suggests an AP-specific network in higher-order cognitive areas. However, when applying multivariate pattern analysis (MVPA), which can capture more fine-grained connectivity patterns, the classification accuracy for AP and non-AP musicians was highest in the left Heschl's gyrus.

Taken together, AP-specific resting-state networks may rely on additional temporo-frontal connections besides the one between the auditory cortex and the DLPFC. Whole-brain analyses provide an opportunity to explore this potential involvement of other regions in an AP-specific network. On the downside, in case of stringent multiple testing correction, whole-brain analyses may miss regional connectivity differences that could have been picked up by ROI-based analyses.

A common limitation of most previous neuroscientific studies comparing AP and non-AP musicians are small sample sizes. This is mostly due to the low prevalence of AP as well as the resource-intensive data acquisition in neuroimaging. Small samples result in low statistical power and unreliable estimates of the true effect (Button et al., 2013). Therefore, studies with larger samples are urgently needed to advance our understanding of the neural underpinnings of AP.

Using a large sample of musicians with AP (n = 54) and without AP (n = 51), we here reevaluate the question of whether AP musicians demonstrate specific functional resting-state connectivity patterns. We recorded resting-state EEG and employed well-established source estimation techniques to measure functional connectivity. For AP research, EEG-based measures might be particularly suited to estimate neurophysiological coactivations during rest since, in contrast to resting-state fMRI recordings, the data is acquired in silence without background noise. The current study further benefits from the application of several connectivity measures (lagged phase synchronization, lagged linear connectivity, and instantaneous linear connectivity), which are each associated with different strengths and weaknesses regarding volume conduction, individual-specific stability, and relation to structural connectivity as described in detail below (see section on 'EEG Source-Level Connectivity' in 'Material and Methods').

To combine the methodological advantages of both ROI-based and whole-brain analyses, we adopted two approaches: (1) We conducted an ROI-based analysis to examine the functional connectivity between the auditory cortex and the DLPFC. This part of the study is a replication of the above-described previous study of our group (Elmer et al., 2015), which had a much smaller sample. (2) We conducted a whole-brain connectivity analysis to explore a potential involvement of other regions besides the auditory cortex and the DLPFC with regard to a more widespread AP-specific network. This analysis was guided by the findings discussed above, which suggest distributed network features in AP musicians comprising brain areas other than the auditory cortex and the DLPFC.

2. Materials and methods

2.1. Participants

Fifty-four AP musicians and 51 non-AP musicians aged 18–44 years participated in the EEG resting-state study. All participants were professional musicians, music students, or highly-trained amateur musicians, who were recruited within a larger research project investigating the neural correlates of AP (Brauchli et al., 2019a, 2019b; Burkhard et al., 2019, 2020; Greber et al., 2018; Leipold et al., 2019a, 2019c, 2019d). The participants were assigned to the two groups based on self-report. Before being invited to the study, participants underwent online testing assessing demographic information, musical experience, and pitch-labeling ability. Based on these data, the two groups were matched for sex, age, handedness, age of onset of musical training, and cumulative hours of musical training over the lifespan.

None of the participants reported any audiological, neurological, or severe psychiatric disorders. Pure-tone audiometry (MAICO ST 20, MAICO Diagnostic, GmBh, Berlin) confirmed normal hearing thresholds in all participants. Self-reported handedness was validated using a German translation of the Annett Handedness Questionnaire (Annett, 1970). To ensure group comparability with regard to general cognitive abilities, intelligence was evaluated using the Mehrfachwahl-Wortschatz-Intelligenztest (MWT-B; Lehrl, 2005). Musical aptitude was estimated using the Advanced Measures of Music Audiation (AMMA; Gordon, 1989). The AMMA consists of 30 pairs of piano melodies. Participants are asked to decide whether the two melodies are identical, different in rhythmical patterns, or different in tonal patterns. The test results in a rhythmical score, a tonal score, and a total score (which equals the sum of rhythmical and tonal score). Characteristics of the two groups are given in Table 1, the results of the statistical comparisons are provided in the Results section (see section 'Statistical Analyses of Demographic and Behavioral Data').

The study was approved by the ethics committee of the canton of Zurich (http://www.kek.zh.ch) and was performed in accordance with

Table 1
Participant characteristics.

	Absolute Pitch Musicians (n = 54)		Non-Absolute Pitch Musicians (n = 51)	
Sex				
Female	27		24	
Male	27		27	
Age (years)	26.67	(5.49)	25.37	(4.49)
Handedness				
Right-handed	47		46	
Left-handed	4		4	
Both-handed	3		1	
Intelligence (MWT-B) [a]	27.69	(5.10)	29.10	(4.64)
Age of Onset of Musical Training (years)	5.93	(2.39)	6.49	(2.44)
Lifetime Cumulative Training (hours) [b]	1.66	(1.22)	1.35	(0.96)
Musical Aptitude (AMMA) [a] – total	66.11	(6.31)	63.35	(6.86)
Musical Aptitude (AMMA) [a] – tonal	32.33	(3.75)	30.45	(4.13)
Musical Aptitude (AMMA) [a] – rhythmical	33.78	(2.83)	32.90	(3.03)
Pitch-labeling Task (%)	76.41	(19.55)	24.04	(18.92)

Annotations. Continuous measures are given as mean (standard deviations in parentheses). Abbreviations: MWT-B = Mehrfachwahl-Wortschatz-Intelligenztest, AMMA = Advanced Measures of Music Audiation. Statistical comparisons for the behavioral and demographic data are listed in the Results section.

[a] Raw scores.

[b] Units are given in 10,000.

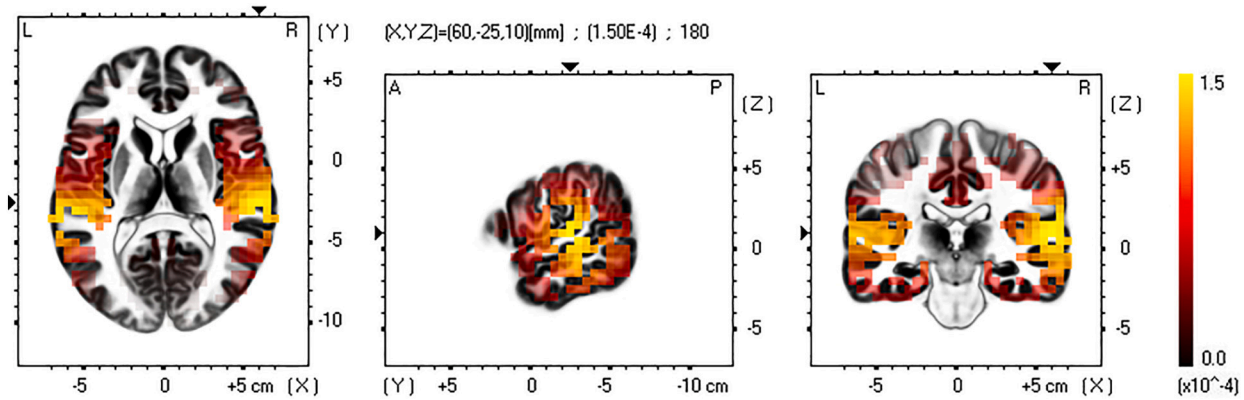

Fig. 1. Validation of the source reconstruction in eLoreta. Current density maps of grand-averaged P1-N1 source activity (80 ms - 170 ms after stimulus onset) evoked by the standard tone C4 (f_0 = 264 Hz) in a passive auditory oddball paradigm (Greber et al., 2018) recorded immediately after the resting state. Shown are horizontal, sagittal, and coronal views (from left to right). Source-level activity was maximal in bilateral auditory regions, confirming reasonable source-estimation accuracy in our setup.

the Declaration of Helsinki. Written informed consent was obtained from all participants.

3. Pitch-labeling task

Pitch-labeling ability was evaluated using a web-based adaptation of a task previously applied by our research group (Oechslin et al., 2010b). The task consisted of 108 trials with pure tones ranging from C3 to B5 (tuning: A4 = 440 Hz). In every trial, 2000 ms of Brownian noise, a 500-ms pure tone, and again 2000 ms of Brownian noise were sequentially presented. Overall, each tone appeared three times in a pseudorandomized presentation order: No tone was repeated in successive trials.

Participants were asked to identify the pitch class (chroma, e.g., G) and octave (e.g., 4) of the pure tone by choosing one label (e.g., G4) out of a list of all possible labels (C3 to B5). Trials could be terminated by clicking on a button and had a maximal duration of 15,000 ms. Pitch-labeling accuracy was calculated as the percentage of correctly identified pitch classes. Octave errors were not penalized, resulting in a chance level of 8.3%.

3.1. EEG recording and preprocessing

For EEG recording, participants were seated in an electrically shielded, dimly lit room and instructed to relax with their eyes closed. The eyes-closed resting-state EEG was recorded for three minutes with a sampling rate of 1000 Hz using a BrainAmp amplifier (Brainproducts, Munich, Germany). The 32 silver/silver-chloride electrodes were mounted on an electrode cap (Easycap, Herrsching, Germany) according to a subset of the 10/10 system (Fp1, Fp2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP9, TP7, CP3, CPz, CP4, TP8, TP10, P7, P3, Pz, P4, P8, O1, Oz, and O2). An electrode on the tip of the nose served both as an online and offline reference. During EEG acquisition, a bandpass filter of 0.1–100 Hz was applied, and electrode impedances were kept below 10 kΩ by application of an abrasive and electrically conductive gel. After recording of the resting-state EEG, participants performed a passive auditory oddball task (published in Greber et al., 2018) and a pitch-processing task (published in Leipold et al., 2019c, 2019d). In the current study, we only report the resting-state data.

The acquired resting-state EEG data were preprocessed using the BrainVision Analyzer software package (Version 2.1, https://www.brainproducts.com/). First, a bandpass filter between 1 and 20 Hz (48 dB/octave), and a notch filter of 50 Hz were applied. Then, a restricted infomax independent component analysis (ICA; Jung et al., 2000) was used to correct eye movement artifacts. Based on visual inspection, noisy channels were excluded from the ICA and interpolated after ICA correction. Finally, the continuous EEG was divided into segments of 2000 ms. Segments with a voltage gradient > 100 μV/ms, an amplitude > 200 μV, or an amplitude < −200 μV were automatically rejected, resulting in a minimum of 62 and maximum of 90 artifact-free segments per participant. The number of artifact-free segments was comparable between AP and non-AP musicians (mean number of segments for AP musicians = 88.69, mean number of segments for non-AP musicians = 89.67; $t_{(59.71)} = -1.66$, $p = .10$, $d = 0.32$).

3.2. EEG source-level estimation

To compute source-level EEG functional connectivity, the EEG segments were imported into the sLORETA/eLORETA (standardized/exact low-resolution brain electromagnetic tomography) toolbox (Version v20151222, http://www.uzh.ch/keyinst/loreta.htm). There, the neural generators of the electric potential differences on the scalp were estimated using the eLORETA algorithm (Pascual-Marqui et al., 2011), a linear, weighted minimum inverse solution with exact localization to point sources. eLORETA uses a realistically shaped head model (Fuchs et al., 2002) based on the Montreal Neurological Institute (MNI) 152 template (Mazziotta et al., 2001) for source reconstruction. The three-dimensional cortical solution space is restricted to gray matter and comprises 6239 voxels with a size of 5 × 5 × 5 mm^3. To validate the accuracy of the source reconstruction, we used EEG data from the passive auditory oddball task performed by the same participants immediately after the resting-state recording (Greber et al., 2018). Participants were instructed to focus their attention on a silent movie and to ignore the simultaneously presented piano tones. Based on the grand average over all participants, we estimated the source activity of the P1-N1 complex (80 ms - 170 ms after stimulus onset) of the event-related potential evoked by the standard tone C4 (piano tone with a fundamental frequency f_0 = 264 Hz). Current density was maximal in bilateral auditory cortices (see Fig. 1), confirming that the eLORETA algorithm performed as intended on our data.

3.3. EEG source-level connectivity

Based on the estimated source-level activity of the EEG resting-state segments, we conducted two types of connectivity analyses: an ROI-based replication analysis and an exploratory whole-brain network analysis. For both analyses, source-level EEG functional connectivity was evaluated with lagged phase synchronization, lagged linear connectivity, and instantaneous linear connectivity. Lagged phase synchronization is the connectivity measure used in Elmer et al.'s (2015)

study. It quantifies the similarity between the normalized Fourier transforms of two signals (i.e. the time series in one brain region and the time series in another brain region) at a specific frequency after removal of the instantaneous, zero-phase contribution. It is a measure of non-linear dependency, is insensitive to amplitude information, and takes values between zero (independence) and one (perfect similarity). The two additionally analyzed connectivity measures, on the other hand, describe the linear coherence-type similarity between two signals at a specific frequency and incorporate both phase and amplitude information. They are also non-negative but have no upper bound (i.e., infinity corresponds to perfect similarity). Their sum equals the total linear connectivity, whereby the lagged part is only minimally affected by non-physiological artifacts, as for example volume conduction and the low spatial resolution (Pascual-Marqui, 2007; Pascual-Marqui et al., 2011). Contrary to lagged measures, instantaneous measures of connectivity are contaminated with non-physiological artifacts. Yet, they have been shown to surpass lagged measures in biometric identification of individuals (Valizadeh et al., 2019) and in the proportion of variance explained by structural connectivity (Finger et al., 2016). Furthermore, instantaneous connectivity measures have been successfully used to obtain meaningful expertise-related resting-state networks in previous studies (e.g., Jäncke and Langer, 2011; Klein et al., 2015, 2018). Hence, (near) zero-lag dependency seems to carry some relevant physiological information that is not fully captured by lagged measures. For instance, a recent study using intracranial recordings found that inter-hemispheric connectivity between homologous regions is often zero-lagged (preprint: O'Reilly and Elsabbagh, 2020). The use of the described connectivity measures enabled us to examine phase-only and phase-amplitude, as well as zero-lag and lagged connectivity differences between the two groups.

For the replication analysis, we defined four ROIs in the cortical solution space using the centroid voxels reported in Elmer et al.'s study (2015; see Fig. 3-A). In each hemisphere, one ROI was placed in the auditory cortex (Brodmann Area [BA] 41/42, xyz coordinates in mm: ± 54, −25, 10) and one ROI was placed in the DLPFC (BA 9/10/46, xyz coordinates in mm: ± 25, 45, 24). As in the original study, EEG functional connectivity between the two ROIs in each hemisphere was evaluated in the theta frequency band (4–7 Hz).

For the exploratory whole-brain network analysis, we computed lagged phase synchronization, linear lagged connectivity, and linear instantaneous connectivity between the centroid voxels of all 84 BAs as implemented in the sLoreta/eLoreta toolbox. Here, we included four frequency bands: theta (4–7 Hz), alpha (8–12 Hz), lower beta (13–21 Hz), and upper beta (22–30 Hz).

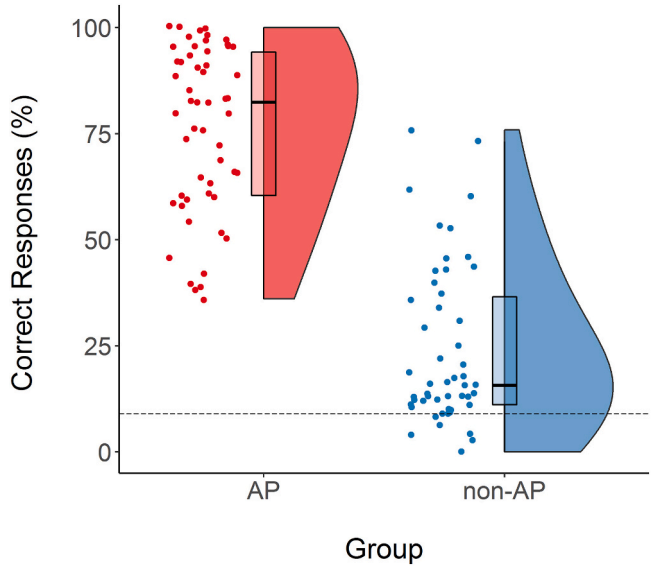

Fig. 2. Pitch-labeling scores for AP (n = 54) and non-AP (n = 51) musicians. Because octave errors were disregarded, the chance level was 8.33% (dashed line). Abbreviations: AP = absolute pitch.

3.4. Data availability

Demographic and behavioral data, EEG raw data, EEG connectivity values, mean network values, and the networks found in the whole-brain analysis with all thresholds are available online at https://dx.doi.org/10.17605/OSF.IO/HBZ28.

3.5. Statistical analysis

We performed (1) statistical analyses of the demographic and behavioral data, (2) replication analyses of the EEG functional connectivity between the auditory cortex and the DLPFC, and (3) network-based analyses of whole-brain EEG functional connectivity.

If not otherwise specified, the analyses were performed using R (version 3.4.3; https://www.r-project.org; R Core Team, 2017). Frequentist Analyses of variance (ANOVAs) were computed using the R package ez (version 4.4.0; https://cran.r-project.org/web/packages/ez/index.html; Lawrence, 2016). Unless otherwise stated, the significance level α was set to 0.05. We report effect sizes as generalized eta-squared η^2_G (Bakeman, 2005) for ANOVAs and as Cohen's d (Cohen, 1988) for t-tests.

3.5.1. Statistical analyses of demographic and behavioral data

The musical aptitude test AMMA was analyzed with a 2 × 2 ANOVA with factors Group (AP and non-AP) and Score Subtype (tonal and rhythmical). All other participant characteristics and behavioral data were analyzed using two-tailed Welch's t-tests.

3.5.2. EEG ROI-based replication analyses

For the ROI-based replication analysis, we used both frequentist and Bayesian statistics. The frequentist analysis exactly replicated the statistical methods used in the original study (Elmer et al., 2015). However, frequentist analyses are limited in that they only permit the rejection of the null hypothesis (H0) but not of the alternative hypothesis (H1). Non-significant results cannot be interpreted as evidence for the absence of an effect. In contrast, Bayesian statistics quantify the evidence both for and against H0 (Dienes, 2011, 2014; Lee and Wagenmakers, 2013; Rouder et al., 2009), which is especially useful for the interpretation of non-significant results (Dienes, 2014) and for the evaluation of replication success (Anderson and Maxwell, 2016). Thus, we computed Bayes factors in addition to the frequentist analysis. Bayes factors compare the (marginal) likelihood of the data under one hypothesis (e.g., H0) with the (marginal) likelihood of the data under another hypothesis (e.g., H1). The relative evidence for one hypothesis as expressed by a Bayes factor can be readily interpreted: A Bayes factor of $BF_{10} = 5$ (or the inverse $\frac{1}{BF_{10}} = BF_{01} = 0.2$) means that the data is five times more likely to occur under H1 than under H0.

For the frequentist replication analyses, the lagged phase synchronization values were subjected to a 2 × 2 ANOVA with factors Group (AP and non-AP) and Hemisphere (left and right). We also computed a one-tailed Welch's t-test to specifically examine the group difference in the left hemisphere, in which the original study found higher connectivity in AP. In addition to the group statistics, we computed one-sided partial correlations for AP musicians between pitch-labeling accuracy and left hemispheric connectivity adjusted for the age of onset of musical training.

Bayes factors for Bayesian ANOVAs (BANOVAs), Bayesian t-tests, and Bayesian correlations were computed using the R package BayesFactor (version 0.9.12–4.2; https://cran.r-project.org/web/packages/BayesFactor/index.html; Morey et al., 2018). We used the default priors (a Cauchy distribution centered around zero with a scale

parameter of 0.707) with the default number of iterations (n = 10,000). Since effect sizes are often inflated in studies with small sample sizes, we refrained from using scale-informed priors based on the effect sizes of the original study (Button et al., 2013; Halsey et al., 2015; Ioannidis, 2008). To confirm the robustness of the results, we tested a variety of additional priors with scale parameters between 0.5 (medium) and 1 (ultrawide); the results suggested the same conclusions as reported here.

For the BANOVAs, Bayes factors of the two main effects (group and hemisphere) were assessed by comparing the model with one factor (e.g., group + subject) to the model with both factors (e.g., group + hemisphere + subject). Interaction effects were assessed by comparing the full model (group + hemisphere + group * deviation + subject) to the model without the interaction effect (group + hemisphere + subject). The Bayes factors reported for the one-sided correlation analyses do not account for the age of onset of musical training.

Extending the analyses of the original study, we analyzed two additional connectivity measures (lagged linear connectivity and instantaneous linear connectivity) to check whether the effect generalizes to other measures of functional connectivity. We report one-sided Welch's t-tests and Bayesian t-tests, and correlations for both hemispheres for all measures as described above.

3.5.3. EEG whole-brain network-based analyses

While the literature- and hypothesis-based definition of two centroids per hemisphere mitigates the multiple comparison problem, it carries the risk of missing other meaningful connections. For this reason, we additionally applied a less-restrictive, exploratory approach to investigate the resting-state EEG data. The whole-brain eLORETA output matrices (84 centroids of 84 BAs) were subjected to group comparisons using the network-based statistic (NBS) toolbox (Zalesky et al., 2010; http://www.nitrc.org/projects/nbs/) in MATLAB (version R2017b; https://www.mathworks.com/products/matlab.html). The analysis was performed separately for the four frequency bands of interest (theta, alpha, lower beta, and upper beta) and the three connectivity measures (lagged phase synchronization, lagged linear connectivity, and instantaneous linear connectivity). The NBS method provides a control for the family-wise error (FWE) rate when testing each connection between many ROIs. It applies the same principles as nonparametric cluster-based thresholding conventionally used in fMRI analyses (Nichols and Holmes, 2001). By considering interconnectedness in the topological space, NBS treats networks holistically and does not declare significance for individual connections.

To compare the individual connectivity matrices between the groups, we used the t-test module in NBS for both one-tailed contrasts (1, −1 and −1, 1). First, this module computed t-test statistics for each pairwise association between the 84 ROIs. Edges exceeding a specified threshold formed a suprathreshold network if connected with each other. The size (i.e., the number of edges) of the largest observed suprathreshold network was subjected to permutation testing. For a total of 5000 permutations, the group labels of the participants were randomly exchanged, and the analysis was repeated using the same threshold. From each permutation step, the size of the largest suprathreshold network was stored to form an empirical estimate of the null distribution. The p-value of the observed network was estimated by counting the permutations that yielded the same or a bigger maximal network size and dividing this count by the total number of permutations. Thus, the reported p-values are FWE corrected only for the number of ROIs. We applied no additional correction for the number of NBS tests performed because of the exploratory nature of the analysis (Althouse, 2016; Bender and Lange, 2001).

Because we were interested in middle (d ≈ 0.4) to large (d ≈ 0.8) effect sizes on the level of individual links, we tested the connectivity matrices for the corresponding thresholds between t = 2.0 and t = 4.0 in increments of 0.1. For each separate analysis (four frequency bands, three connectivity measures, two contrasts), we report all thresholds at which a network with p < .05 emerged. We describe one of these networks in detail, which is representative of the networks obtained using those thresholds. All networks with p < .05 are available online at https://dx.doi.org/10.17605/OSF.IO/HBZ28. The reported networks were visualized using the BrainNet Viewer software (version 1.53; http://www.nitrc.org/projects/bnv/) in MATLAB (Version R2017b, https://www.mathworks.com/products/matlab.html). The Harvard-Oxford cortical atlas and the Juelich Histological atlas as implemented in FSL (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL) were used to specify the brain regions underlying the involved nodes.

After identification of the networks, we analyzed the relationship between the corresponding mean network values and pitch-labeling performance using R (version 3.4.3; https://www.r-project.org; R Core Team, 2017). We computed both frequentist and Bayesian correlations (two-sided, non-partial) for each group separately.

4. Results

4.1. Results of demographic and behavioral analyses

AP and non-AP musicians were comparable in age ($t_{(100.97)}$ = 1.33, p = .19, d = 0.26), intelligence ($t_{(102.86)}$ = −1.49, p = .14, d = 0.29), age of onset of musical training ($t_{(102.42)}$ = −1.20, p = .23, d = 0.23), and cumulative musical training hours over the lifespan ($t_{(99.71)}$ = 1.43, p = .16, d = 0.28). The analysis of the AMMA scores (measuring musical aptitude) yielded a main effect of Group ($F_{(1,103)}$ = 4.60, p = .034, η^2_G = 0.04), a main effect of Score Subtype ($F_{(1,\ 103)}$ = 79.27, p < .001, η^2_G = 0.07), and an interaction effect ($F_{(1,\ 103)}$ = 5.37, p = .023, η^2_G = 0.005). Post hoc t-tests (Bonferroni corrected α = 0.25) revealed that the AP musicians were comparable to non-AP musicians in the rhythmical score ($t_{(101.38)}$ = 1.53, p = .13, d = 0.30) but had a higher tonal score ($t_{(100.61)}$ = 2.44, p = .016, d = 0.48). As expected, AP musicians outperformed non-AP musicians in the pitch-labeling task ($t_{(102.93)}$ = 13.95, p < .001, d = 2.72; see Fig. 2).

4.2. Results of ROI-based replication analyses

The ROI-based replication analysis of lagged phase synchronization – the measure used in the original study (Elmer et al., 2015) – in the theta frequency band between the auditory cortex and the DLPFC revealed no evidence for a main effect of Group ($F_{(1,\ 103)}$ = 1.86, p = .18, η^2_G = 0.01, BF_{01} = 3.39), no evidence for a main effect of Hemisphere ($F_{(1,\ 103)}$ = 0.06, p = .81, η^2_G < 0.001, BF_{01} = 8.90), and no evidence for a Group × Hemisphere interaction ($F_{(1,\ 103)}$ = 0.01, p = .91, η^2_G < 0.001, BF_{01} = 6.69). Lagged-synchronization values are shown in Fig. 3-B and posterior distributions of the BANOVA are illustrated in Fig. 3-D. The planned one-tailed t-test did not reveal evidence for a difference between the two groups in the left hemisphere ($t_{(102.75)}$ = −0.90, p = .81, d = 0.18, BF_{01} = 8.49; see Fig. 3-B). There was also no evidence for a positive relationship between pitch-labeling performance and left-hemispheric lagged phase synchronization in AP musicians (r_p = −0.034, p = 1.00, BF_{01} = 4.26; see Fig. 3-C).

Additional analyses of resting-state connectivity between the auditory cortex and the DLPFC in AP musicians based on lagged linear connectivity and instantaneous linear connectivity also revealed no evidence for differences between the two groups. All results of the group comparisons for each hemisphere are shown in detail in Table 2. There was also no evidence for a positive relationship between pitch-labeling performance and resting-state connectivity between the auditory cortex and the DLPFC in AP musicians. The results of the correlational analyses are shown in Table 3.

4.3. Results of whole-brain network-based analyses

The network-based analyses of the 84-ROI connectivity matrices revealed group differences in three measure × frequency combinations

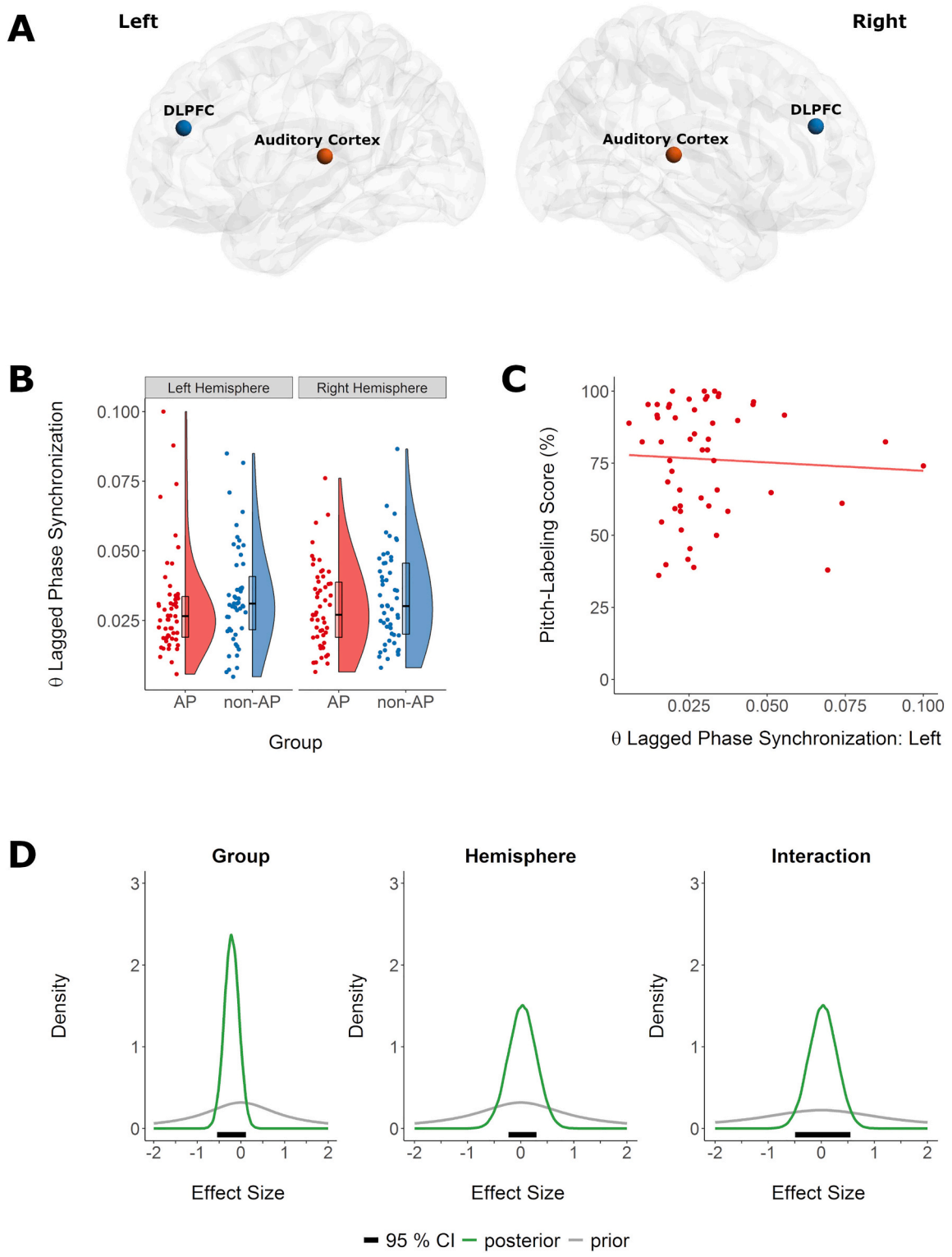

Fig. 3. Replication analysis of theta lagged phase synchronization between the auditory cortex and the DLPFC during EEG resting state. A) Localization of the four ROIs. B) There was no evidence for a difference in theta lagged phase synchronization values between AP musicians (red) and non-AP musicians (blue). C) There was no evidence for a positive correlation between left-hemispheric theta lagged phase synchronization and performance in the pitch-labeling task in AP musicians. D) Prior (gray) and posterior (green) distributions of the standardized effects (relative to the standard deviation of the error term) of the factors Group and Hemisphere on theta lagged phase synchronization. The Bayesian 95% credible interval describes the interval that includes the true value with a probability of 95%, given the data and the assumed model. Abbreviations: 95% CI = Bayesian 95% credible interval, AP = absolute pitch, DLPFC = dorsolateral prefrontal cortex, ROI = region of interest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(see Fig. 4): AP musicians showed hyperconnected resting-state networks in (A) lagged linear connectivity in lower beta, (B) in instantaneous linear connectivity in lower beta, and (C) in instantaneous linear connectivity in theta. No networks with $p < .05$ were observed in lagged phase synchronization or in any of the other tested frequency bands of lagged and instantaneous linear connectivity. The analyses did

Table 2
Group comparisons of theta-band connectivity between the auditory cortex and the DLPFC.

Connectivity Measure	Hemisphere	AP	Non-AP	*p*-value	Cohen's *d*	BF_{01}
Lagged phase synchronization	Right	0.030 (0.015)	0.033 (0.017)	0.88	0.23	9.77
	Left	0.030 (0.018)	0.034 (0.018)	0.81	0.18	8.49
Lagged linear connectivity	Right	0.046 (0.029)	0.049 (0.031)	0.70	0.11	6.96
	Left	0.043 (0.028)	0.051 (0.032)	0.91	0.27	10.64
Instantaneous linear connectivity	Right	0.967 (0.773)	0.810 (0.466)	0.10	0.25	1.37
	Left	0.787 (0.415)	0.756 (0.433)	0.35	0.07	3.55

Annotations. One-sided Welch's *t*-tests were applied to compare AP and non-AP musicians (hypothesis AP > non-AP). Group values for AP and non-AP musicians are given as mean (standard deviation in parentheses). Lagged phase synchronization was the measure used in the original study (Elmer et al., 2015). Abbreviations: AP = absolute pitch, DLPFC = dorsolateral prefrontal cortex.

Table 3
Correlations between pitch-labeling performance and theta-band connectivity in AP musicians.

Connectivity measure	Hemisphere	*r*	$p_{one\text{-}sided}$	BF_{01}
Lagged phase synchronization	Right	0.160	0.12	0.99
	Left	−0.034	1.00	4.26
Lagged linear connectivity	Right	0.001	0.50	2.49
	Left	−0.157	1.00	3.86
Instantaneous linear connectivity	Right	−0.199	1.00	6.70
	Left	−0.054	1.00	3.86

Annotations. One-sided partial correlations (*r* and *p* adjusted for age of onset of musical training; hypothesis higher pitch-labeling score is associated with stronger connectivity). Theta-band connectivity was evaluated between the auditory cortex and the DLPFC. Lagged phase synchronization was the measure used in the original study (Elmer et al., 2015). Abbreviations: AP = absolute pitch, DLPFC = dorsolateral prefrontal cortex.

also not reveal any networks with decreased connectivity in AP musicians compared to non-AP musicians.

(A) In lagged linear connectivity in the lower beta frequency band, networks with $p < .05$ were found for all tested thresholds between $t = 2.0$ (76 nodes, 423 edges) and $t = 3.7$ (2 nodes, 1 edge). We report the network at $t = 3.0$, visualized in Fig. 4-A. At this threshold, 13 nodes and 14 edges contributed to the network ($p = .037$, FWE corrected for the number of ROIs). The brain regions underlying the involved nodes are listed in Table 4. Nodes in the left temporal lobe (auditory regions, planum temporale) were connected to nodes in the frontal lobe both intrahemispherically (left middle and superior frontal gyrus) and interhemispherically (right middle/ superior frontal gyrus, BA 6). Within the right hemisphere, nodes in the frontal lobe (middle frontal gyrus, superior frontal gyrus, inferior frontal gyrus), in the parietal operculum, in the insular cortex, and in the middle temporal gyrus contributed to the network. Two-sided correlations revealed no evidence for a relationship between mean network values and pitch-labeling performance within AP musicians ($r = 0.095$, $p = .49$, $BF_{01} = 2.63$) or within non-AP musicians ($r = 0.075$, $p = .60$, $BF_{01} = 2.80$).

(B) In instantaneous linear connectivity in the lower beta frequency band, networks with $p < .05$ were obtained at thresholds between $t = 2.0$ (77 nodes, 411 edges) and $t = 3.0$ (19 nodes, 23 edges), and at $t = 3.6$ (4 nodes, 3 edges) and $t = 3.7$ (3 nodes, 2 edges). The relatively widespread network at $t = 3.0$ ($p = .044$, FWE corrected for number of ROIs; see Table 5 and Fig. 4 B) consisted of nodes in the occipital lobe (visual cortex, occipital pole, precuneus), in subcortical regions (hippocampal and parahippocampal regions), in the temporal lobe (inferior temporal gyrus, middle temporal gyrus, temporal pole, planum temporale/auditory cortex), and in the frontal lobe (frontal pole, inferior frontal gyrus). There was no evidence for a correlation between mean network values and pitch-labeling performance within the AP group ($r = 0.004$, $p = .97$, $BF_{01} = 3.25$) or within the non-AP group ($r = 0.008$, $p = .96$, $BF_{01} = 3.17$).

(C) In instantaneous linear connectivity in the theta frequency band, NBS revealed networks with $p < .05$ at thresholds between $t = 3.1$ (11 nodes, 15 edges) and $t = 3.5$ (7 nodes, 6 edges). At a middle-level threshold of $t = 3.3$, the network ($p = .032$, FWE corrected for number of ROIs) compromised of 8 nodes in temporal and perisylvian regions (middle temporal gyrus, superior temporal gyrus, planum temporale, auditory cortex, and parietal operculum) and of 10 interhemispheric connections. The network nodes are described in detail in Table 6, and the network is visualized in Fig. 4-C. Similar to the other two networks, there was no evidence for a relationship between mean network values and pitch-labeling performance in either AP ($r = 0.070$, $p = .63$, $BF_{01} = 2.92$) or non-AP musicians ($r = -0.16$, $p = .27$, $BF_{01} = 1.83$).

5. Discussion

This study investigated EEG resting-state connectivity in AP and non-AP musicians to provide insights into the role of perceptual and cognitive processes in AP. In a two-part analysis, we first attempted to replicate our previous finding of increased theta resting-state connectivity between the left auditory cortex and the left DLPFC (Elmer et al., 2015). In the second part, we performed an exploratory whole-brain analysis to evaluate whether the auditory cortex and the DLPFC are part of a larger AP-specific resting-state network.

In the ROI-based replication analysis, we found no evidence for an increase in theta-band lagged phase synchronization between the auditory cortex and the DLPFC in AP musicians compared to non-AP musicians. Bayes factor analyses favored the null hypothesis of no group differences (BF > 8). Similar results were obtained for two additionally analyzed connectivity measures. There was also no evidence for a positive relationship between pitch-labeling proficiency and left-hemispheric theta connectivity in the AP group. The whole-brain analysis provided weak evidence in favor of hyperconnected networks in AP musicians in the theta and lower-beta frequency bands using instantaneous linear connectivity, and in the lower-beta frequency band using lagged linear connectivity.

5.1. ROI-based replication analyses: auditory cortex and DLPFC

In the ROI-based analysis, we did not replicate the previous finding (Elmer et al., 2015) of increased left-hemispheric temporo-frontal connectivity in AP musicians. This corresponds at least partly with previous reports on functional connectivity in AP. While the connectivity of the auditory cortex in AP has been addressed by several

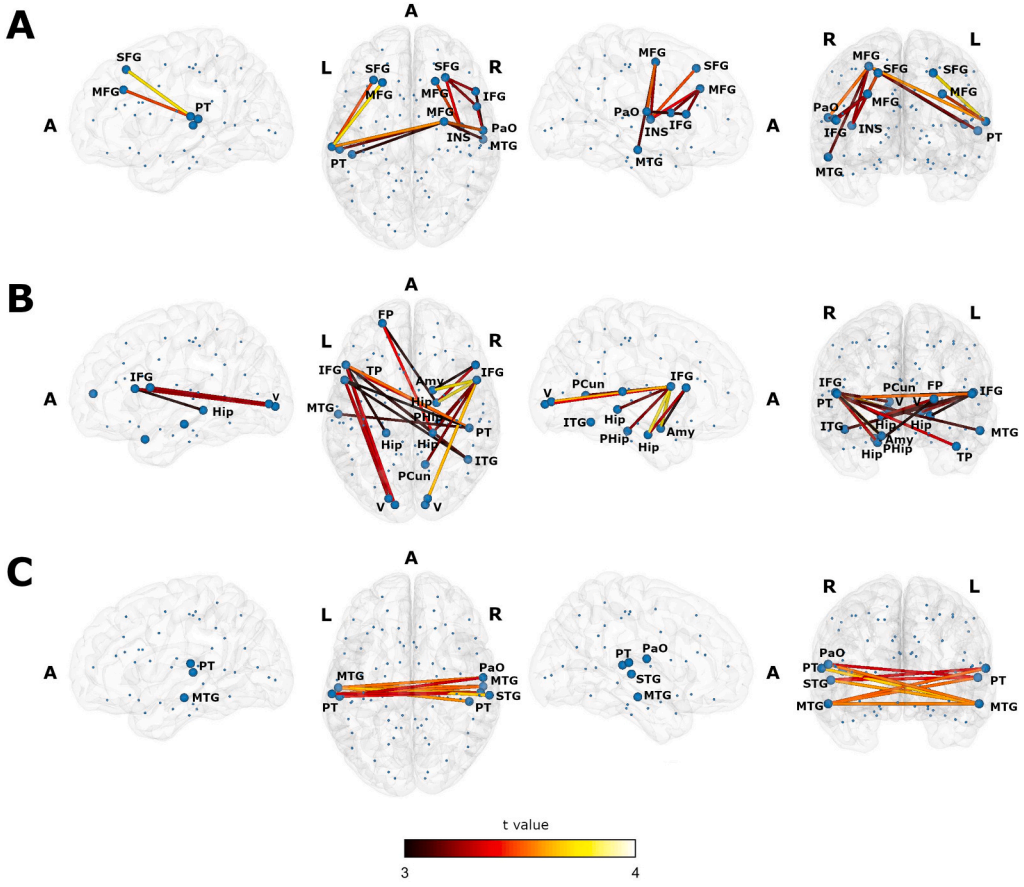

Fig. 4. Lateral, axial and coronal views of the three obtained resting-state networks. All three networks show increased undirected connectivity in AP musicians compared to non-AP musicians. Blue spheres represent the centroids of the 84 Brodmann Areas. Nodes contributing to the network are depicted by enlarged spheres. The color of the edges corresponds to the *t*-value. A) The network in lagged linear connectivity in lower beta. B) The network in instantaneous linear connectivity in lower beta. C) The network in instantaneous linear connectivity in theta.
Abbreviations: A = anterior, Amy = amygdala, AP = absolute pitch, FP = frontal pole, Hip = hippocampus subiculum, IFG = inferior frontal gyrus, INS = insular cortex, ITG = inferior temporal gyrus, L = left hemisphere, MFG = middle frontal gyrus, MTG = middle temporal gyrus, PaO = parietal operculum, PCun = precuneus cortex, PHip = parahippocampal gyrus, PT = planum temporale, R = right hemisphere, SFG = superior frontal gyrus, STG = superior temporal gyrus, TP = temporal pole, V = visual cortex. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

previous studies (e.g., Jäncke et al., 2012; Loui et al., 2011, 2012), much less is known about the DLPFC. For instance, a recent functional magnetic resonance imaging (fMRI) study found differential local connectivity patterns in the left auditory cortex during resting state but neither local nor global connectivity differences in the DLPFC between musicians with and without AP (Brauchli et al., 2019a). In another fMRI study, the Heschl's gyrus was functionally connected to various auditory and non-auditory regions during passive tone listening in the AP group (Wengenroth et al., 2014). However, no evidence was found for an AP-specific synchronization between the auditory cortex and the DLPFC. Furthermore, Kim and Knösche (2017b) found no evidence for group differences in resting-state connectivity between the auditory cortex and seeds in the planum temporale, which is part of the dorsal auditory pathway between the auditory cortex and the DLPFC (Rauschecker and Scott, 2009). Alternatively, it has been proposed that the ventral pathway projecting to the inferior frontal gyrus via the anterior temporal lobe might play a more important role in AP processing than the DLPFC (Kim and Knösche, 2017a, 2017b; Leipold et al., 2019b). The only other study besides Elmer et al. (2015) providing some evidence for the importance of a dorsal connection between auditory and frontal regions in AP found a leftward asymmetry of fractional anisotropy measures of the arcuate fasciculus in AP musicians but not in non-AP musicians or non-musicians (Oechslin et al., 2010a). The arcuate fasciculus structurally connects the posterior superior temporal gyrus and the prefrontal cortex (Makris et al., 2005). Taken together, there is not yet much support for increased connectivity between the

Table 4
Brain regions underlying the centroid voxel coordinates of the BAs constituting the lower-beta linear lagged connectivity network (*t* threshold = 3.0 associated with a Cohen's *d* = 0.59).

MNI coordinates (x, y, z)	Brain region	Brodmann area
−22, 28, 49	left superior frontal gyrus	BA 8
−29, 30, 33	left middle frontal gyrus	BA 9
−56, −25, 5	left planum temporale/primary auditory cortex	BA 41
−46, −29, 10	left planum temporale/primary auditory cortex	BA 41
−62, −23, 12	left planum temporale	BA 42
27, −3, 54	right middle frontal gyrus/superior frontal gyrus	BA 6
20, 29, 49	right superior frontal gyrus	BA 8
28, 32, 33	right middle frontal gyrus	BA 9
40, −7, 9	right insular cortex	BA 13
58, −17, −15	right middle temporal gyrus	BA 21
58, −10, 15	right secondary somatosensory cortex/parietal operculum	BA 42
53, 9, 14	right inferior frontal gyrus (Broca's area BA44)	BA 44
52, 21, 13	right inferior frontal gyrus (Broca's area BA44/BA45)	BA 44/45

Annotations. Nodes were assigned to brain regions based on the Harvard-Oxford cortical atlas and the Juelich Histological atlas. Brodmann areas refer to the LORETA output. Abbreviations: BA = Brodmann area.

Table 5
Brain regions underlying the centroid voxel coordinates of the BAs constituting the lower-beta linear instantaneous connectivity network (t threshold = 3.0 associated with a Cohen's d = 0.59).

MNI coordinates (x, y, z)	Brain region	Brodmann area
−22, 54, 9	left frontal pole	BA 10
−12, −90, −1	left visual cortex (V1, V2, V3)/occipital pole	BA 17
−17, −85, 1	left visual cortex (V3)	BA 17
−57, −18, −15	left middle temporal gyrus	BA 21
−19, −33, −4	left hippocampus subiculum	BA 27
−39, 13, −27	left temporal pole	BA 38
−52, 9, 14	left inferior frontal gyrus (Broca's area BA44)	BA 44
−51, 21, 13	left inferior frontal gyrus (Broca's area BA44)	BA 44/45
12, −90, 0	right visual cortex (V1)/occipital pole	BA 17
14, −85, 2	right visual cortex (V1)	BA 17
18, −33, −4	right hippocampus subiculum	BA 27
21, −9, −24	right hippocampus subiculum	BA 28
12, −58, 7	right visual cortex (V1)/precuneus cortex	BA 30
18, 1, −19	right amygdala superficial group/parahippocampal gyrus	BA 34
23, −25, −21	right parahippocampal gyrus	BA 35
46, −54, −14	right inferior temporal gyrus/temporal occipital fusiform cortex	BA 37
47, −29, 10	right planum temporale/primary auditory cortex	BA 41
53, 9, 14	right inferior frontal gyrus (Broca's area BA44)	BA 44
52, 21, 13	right inferior frontal gyrus (Broca's area BA44/BA45)	BA 44/45

Annotations. Nodes were assigned to brain regions based on the Harvard-Oxford cortical atlas and the Juelich Histological atlas. Brodmann areas refer to the LORETA output. Abbreviations: BA = Brodmann area.

Table 6
Brain regions underlying the centroid voxel coordinates of the BAs constituting the theta linear instantaneous connectivity network (t threshold = 3.3 associated with a Cohen's d = 0.65).

MNI coordinates (x, y, z)	Brain region	Brodmann area
−57, −18, −15	left middle temporal gyrus	BA 21
−56, −25, 5	left planum temporale/primary auditory cortex	BA 41
−62, −23, 12	left planum temporale	BA 42
58, −17, −15	right middle temporal gyrus	BA 21
56, −22, 3	right superior temporal gyrus	BA 41
47, −29, 10	right planum temporale/primary auditory cortex	BA 41
63, −24, 12	right planum temporale	BA 42
58, −10, 15	right secondary somatosensory cortex/ parietal operculum	BA 42

Annotations. Nodes were assigned to brain regions based on the Harvard-Oxford cortical atlas and the Juelich Histological atlas. Brodmann areas refer to the LORETA output. Abbreviations: BA = Brodmann area.

auditory cortex and the DLPFC in AP, consistent with the results of the current study.

Some studies suggested that the DLPFC might be involved in the pitch-label association process in AP (Bermudez and Zatorre, 2005; Levitin and Rogers, 2005; Ohnishi et al., 2001; Zatorre et al., 1998). However, a recent fMRI study of our group did not observe an involvement of the DLPFC in AP during a pitch-processing task (Leipold et al., 2019a), casting doubt on the exact role of the DLPFC in pitch labeling. Activity in the DLPFC increased equally in musicians with and without AP between a listening and a labeling condition. Hence, we suggested that the activity in the DLPFC might actually reflect unspecific attentional or executive control processes rather than the label retrieval itself. The inconsistencies in DLPFC activation even during acoustic stimulation might explain to some extent why the increase in functional connectivity between the left auditory cortex and the left DLPFC could not be reliably detected during EEG resting state.

It is important to note that the DLPFC encompasses a rather large cortex region whose exact location and extension are not universally agreed upon (e.g., BA 9/46 Cieslik et al., 2013; BA 8/9/46 O'Reilly, 2010; BA 8/9/46 Plakke and Romanski, 2014; BA 8a/46 Rauschecker, 2011; BA 9/10/46 Teffer and Semendeferi, 2012). By considering only a single centroid within the DLPFC in our replication analysis, we cannot make statements about this broad region as a whole. We can only conclude that there was no evidence for an AP-specific increase in connectivity between the auditory cortex and the DLPFC as it was defined in the original study.

5.2. Whole-brain network-based analyses

The exploratory whole-brain analyses yielded three resting-state networks with enhanced EEG connectivity (i.e., hyperconnectivity) in AP musicians compared to non-AP musicians. We did not find any evidence for networks with decreased connectivity in AP musicians. Several MRI studies have reported functional and structural hyperconnectivity in AP using a variety of both ROI-based and whole-brain methods (Brauchli et al., 2019a; Dohn et al., 2015; Kim and Knösche, 2017b; Loui et al., 2011, 2012; Wengenroth et al., 2014). On the other hand, there is also one report of reduced whole-brain connectivity (i.e., cortical thickness covariance) in AP musicians (Jäncke et al., 2012). Similarly, a recent EEG resting-state study observed global hypoconnectivity (i.e., lower clustering) in AP musicians on the electrode level (Wenhart et al., 2019). A recently published source-level EEG study, however, did not find any evidence for network differences between AP and non-AP musicians during resting state (Brauchli et al., 2019b). In contrast to our study, Brauchli and colleagues analyzed eyes-open instead of eyes-closed resting-state data. Taken together, there is some heterogeneity in the literature as to whether connectivity in AP musicians is increased, decreased, or comparable to non-AP musicians. The greatly varying methods (e.g., imaging modality, structural vs functional, ROI-based vs whole-brain, electrode-level vs source-level, eyes-open vs eyes-closed, dependency measures, different types of connectivity and network analyses, different procedures for AP group assignment) may account for some of the diverging results. Resting-state connectivity of AP musicians might in particular be affected by the imaging modality. In addition to the inherent differences between fMRI and EEG regarding temporal and spatial resolution, there is no background noise during EEG recording. The fMRI scanner noise, on the other hand, might activate some pitch-labeling processes in AP musicians. Further research is necessary to disentangle hyper- and hypoconnectivity in AP and the influence of the respectively used methods.

The three networks we identified in our exploratory whole-brain analysis covered nodes in frontal, temporal, subcortical, and occipital

brain regions. Common features across the three networks were the planum temporale, the inferior frontal gyrus, the parietal operculum, and the middle temporal gyrus. The planum temporale, a secondary auditory region posterior to the Heschl's gyrus, has repeatedly been associated with AP (Burkhard et al., 2020; Keenan et al., 2001; Leipold et al., 2019a; Luders et al., 2004; Ohnishi et al., 2001; Schlaug et al., 1995; Wengenroth et al., 2014; Wilson et al., 2009; Zatorre et al., 1998). While its precise function in AP remains unknown, the planum temporale has been suspected to be involved in the matching of auditory input to internal templates (Griffiths and Warren, 2002). As recently put forward by Leipold et al., 2019a, a similar matching process specifically involving pitch templates might occur in the planum temporale of AP musicians during pitch labeling. The parietal operculum (secondary somatosensory cortex) has also been previously reported in connection with AP; its involvement was presumed to indicate sensorimotor integration (Wengenroth et al., 2014). However, considering the relatively low spatial resolution of EEG and the spatial closeness of the centroid voxels of the parietal operculum and the planum temporale, these nodes might not necessarily show selective neural activations of different brain regions in the present study. The inferior frontal gyrus has repeatedly been implicated in AP (Dohn et al., 2015; Leipold et al., 2019a; McKetton et al., 2019; Schulze et al., 2009; Wengenroth et al., 2014; Zatorre et al., 1998). Because its activity was either increased or decreased in AP musicians depending on the specific task, different functions have been attributed to it, such as a verbal component in AP processing (Wengenroth et al., 2014) or a working memory component in relative-pitch processing (Leipold et al., 2019a). Finally, the middle temporal gyrus has also been previously linked to AP (Burkhard et al., 2019; Kim and Knösche, 2017b; Loui et al., 2011; Wengenroth et al., 2014; Zatorre et al., 1998). The middle temporal gyrus participates in a multitude of functions (for an overview, consider Xu et al., 2015), including higher-order language processes (Friederici, 2002; Hickok and Poeppel, 2007; Oechslin et al., 2010b). In the context of AP, the middle temporal gyrus has been proposed to play a role in accessing stored pitch templates (Loui et al., 2012), in categorizing perceived tones (Burkhard et al., 2019), or in recruiting multimodal codes for extracted pitch information (Zatorre et al., 1998).

The networks were found in the theta (4–7 Hz) and the lower-beta (13 Hz – 21 Hz) frequency range. A number of cognitive functions have been linked to these oscillation rhythms (for a review, see Wang, 2010). For theta, these functions include working memory, memory encoding, and memory retrieval (Albouy et al., 2017; Hsieh and Ranganath, 2014; Ward, 2003), whereas the beta frequency band is involved in sensorimotor integration and top-down signaling (Engel and Fries, 2010; Siegel et al., 2012). These attributed functions are very well in accordance with the brain regions we found contributing to the AP-specific networks.

For all three networks, we found no evidence for a relationship between the mean network connectivity values and pitch-labeling scores within the group of AP musicians. Similarly, a recent fMRI resting-state study from our research project showed no significant correlations between the connectivity measures and pitch-labeling scores within the AP group (Brauchli et al., 2019a). As argued there with reference to a large-scale behavioral study (Athos et al., 2007), a possible explanation for this lack of correlation might be that AP is a distinct rather than a continuous ability. Another possibility is that even within the AP group, different strategies were used to solve the pitch-labeling task. Such individual differences beyond a common mechanism might explain the rather large variance in pitch-labeling scores within the AP musicians and, consequently, the lack of correlation with the network values. Finally, in light of the number of tests performed, it is also possible that the identification of the networks is affected by the type I error, and as a result, the mean network values do not significantly correlate with the pitch-labeling scores.

Overall, the nodes shared among the three networks corroborate the importance of perisylvian areas in AP, including prefrontal regions. The non-overlapping nodes of the networks might indicate the use of a widespread, possibly multisensory network. However, considering the number of exploratory NBS analyses that did not yield any evidence for group differences, the strength of evidence for hyperconnectivity during eyes-closed resting-state EEG remains weak.

5.3. Limitations

Several general limitations apply to both the ROI-based and the whole-brain analysis. First, EEG source localization might be relatively imprecise when based on a small number of electrodes (Baillet, 2017; Srinivasan et al., 1998). To be sufficiently confident of the source reconstruction, we checked localization accuracy during acoustic stimulation, which confirmed that the eLORETA algorithm performed well on our data. Additionally, previous studies have verified the source reconstruction accuracy of the LORETA toolbox even for small numbers of scalp electrodes using intracranial electrode recording (Zumsteg et al., 2005, 2006). Second, the connectivity measures used in the analyses do not distinguish between direct and indirect connections (common input problem: Bastos and Schoffelen, 2016). Thus, connectivity between two nodes could have been mediated by a third source not included in the analysis. Lastly, caution must be applied when generalizing resting-state networks to active processing. As pointed out by Petersen and Sporns (2015), it could be that even brain networks activated by daily tasks (e.g., reading) are not necessarily expressed during resting state if, for instance, the contributing regions are also used by various other tasks. Thus, future connectivity analyses during active tasks are vital for a better understanding of the networks specifically involved in the process of pitch labeling in AP.

Additional limitations specifically apply to the ROI-based replication analysis. While both the current and the original study relied on self-reports with respect to group assignment to the AP and non-AP groups and retrospectively tested this group assignment using a pitch-labeling test, there are still some differences in terms of the used samples. First, we changed the assessment of the questionnaires and the pitch-labeling task from paper-pencil to online at home to lower the on-site testing workload for our participants. Second, due to the online implementation, the pitch-labeling task had to be slightly modified: Trials could last up to 15 s instead of a fixed duration of 5 s in the paper-pencil implementation of the original study. A pilot test showed that this modification was necessary for participants to be able to solve the multiple-choice format with 36 response options. Third, contrary to the original study, AP musicians scored higher than non-AP musicians in the tonal part of the musical aptitude test (AMMA) in the present study. Whilst statistically significant, this group difference was small in absolute numbers (less than 2 points out of a maximal score of 40 points), and the means were similar to those of the original sample. Finally, there was no overlap between the two groups in pitch-labeling scores in the original study (all non-AP musicians had less than 20% correct, all AP-musicians had more than 35% correct), but there was an overlap in our sample (highest score among non-AP musicians was 75.9%, the lowest score among AP musicians was 36.1%). This could be attributed to less homogenous groups but might also be due to the larger sample size or the longer trial duration in our pitch-labeling task: Because the participants had more time to respond, they might have used their relative-pitch ability to solve the task. It is conceivable that highly trained non-AP musicians can perform well under these circumstances. The difference between the two studies regarding the overlap in pitch-labeling scores seems to mostly stem from such well-performing non-AP musicians in the current study. To prevent non-AP musicians from using relative-pitch cues in pitch-labeling tasks, future studies should consider using non-harmonic and distorted interference stimuli between the tones as proposed by Wengenroth et al. (2014). AP musicians showed a similarly large range of pitch-labeling scores in the current and the original study. Unpublished data from our lab suggests a strong correlation ($r = 0.7$) between the online pitch-labeling test used in the

current study and the on-site test used in the original study within AP musicians (n = 39). Although this correlation is strong there is still some unexplained variance, which might indicate that different cognitive functions have been involved during the performance of these different pitch-labeling task variants. Whether these suspected differences between the previous and the current study might be responsible for the different findings is disputable and should be examined in further experiments. We also found no evidence for a positive correlation between the pitch-labeling scores and the connectivity values of the ROI-based analysis within the AP group, which would have supported the importance of the connection between the auditory cortex and the DLPFC for AP.

5.4. Conclusion

Using the ROIs defined in Elmer et al.'s (2015) study, we did not replicate an AP-specific increase in resting-state connectivity between the auditory cortex and the DLPFC in the theta frequency band. The exploratory whole-brain analyses provided weak evidence for increased functional interactions among distributed brain areas in AP in the theta and lower-beta frequency bands. These areas comprised mainly auditory and frontal brain regions but also included regions that engage in sensorimotor and visual processes. Future task-based studies using acoustic stimulation are necessary to confirm the involvement of these regions and to clarify their specific role in the pitch-labeling process.

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Author contributions

S.L, M.G., C.K., and L.J. designed research; M.G. performed research; M.G., and S.S. analyzed data; M.G., S.L., S.S., C.K., and L.J. wrote the paper.

Declaration of competing interest

The authors declare no conflict of interest.

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Chapter 4 Empirical Work: Article 3

Suppression of pitch labeling: no evidence for an impact of absolute pitch on behavioral and neurophysiological measures of cognitive inhibition in an auditory Go/Nogo task

Marielle Greber, Lutz Jäncke

Abstract

Pitch labeling in absolute pitch (AP), the ability to recognize the pitch class of a sound without an external reference, is effortless, fast, and presumably automatic. Previous studies have shown that pitch labeling in AP can interfere with task demands. In the current study, we used a cued auditory Go/Nogo task requiring same-different decisions to investigate both behavioral and electrophysiological correlates of increased inhibitory demands related to automatic pitch labeling. The task comprised two Nogo conditions: a Nogo condition with pitch differences larger than one semitone, and a second Nogo condition with pitch differences of only a quarter semitone. The first Nogo condition tested if auditory-related inhibition processes are generally altered in AP musicians. The second Nogo condition tested the suppressibility of the pitch labeling by means of a Stroop-like effect: The two tones belonged to the same pitch class but were not identical in terms of tone frequency. If pitch labeling cannot be suppressed, the conflicting information would be expected to increase the inhibitory load in AP musicians.

Our data provided no evidence for an increased difficulty to inhibit a prepotent response or to suppress conflicting pitch-labeling information in AP: AP musicians showed similar commission error rates as non-AP musicians in both Nogo conditions. N2d and P3d amplitudes of AP musicians were also comparable to those of non-AP musicians. The event-related potentials were, however, modulated by the Nogo condition, probably indicating an effect of stimulus similarity. It is possible that, depending on the context, pitch labeling in AP musicians is not entirely automatic and can be suppressed.

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Suppression of Pitch Labeling: No Evidence for an Impact of Absolute Pitch on Behavioral and Neurophysiological Measures of Cognitive Inhibition in an Auditory Go/Nogo Task

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Pitch labeling in absolute pitch (AP), the ability to recognize the pitch class of a sound without an external reference, is effortless, fast, and presumably automatic. Previous studies have shown that pitch labeling in AP can interfere with task demands. In the current study, we used a cued auditory Go/Nogo task requiring same/different decisions to investigate both behavioral and electrophysiological correlates of increased inhibitory demands related to automatic pitch labeling. The task comprised two Nogo conditions: a Nogo condition with pitch differences larger than one semitone, and a second Nogo condition with pitch differences of only a quarter semitone. The first Nogo condition tested if auditory-related inhibition processes are generally altered in AP musicians. The second Nogo condition tested the suppressibility of the pitch labeling using a Stroop-like effect: the two tones belonged to the same pitch class but were not identical in terms of tone frequency. If pitch labeling cannot be suppressed, the conflicting information would be expected to increase the inhibitory load in AP musicians. Our data provided no evidence for an increased difficulty to inhibit a prepotent response or to suppress conflicting pitch-labeling information in AP: AP musicians showed similar commission error rates as non-AP musicians in both Nogo conditions. N2d and P3d amplitudes of AP musicians were also comparable to those of non-AP musicians. The event-related potentials (ERPs) were, however, modulated by the Nogo condition, probably indicating an effect of stimulus similarity. It is possible that, depending on the context, pitch labeling in AP musicians is not entirely automatic and can be suppressed.

Keywords: absolute pitch (AP), Go/Nogo, musicians, auditory, inhibition, event-related potential (ERP)

INTRODUCTION

Pitch is one of the main perceptual properties of musical tones. Most people perceive pitch not in absolute but rather in relative terms, i.e., they register whether a pitch is higher or lower compared to a previous pitch. Professional musicians are further trained to determine the exact amount of the relative difference between two pitches in terms

of musical intervals. Using this so-called relative-pitch (RP) ability, most musicians can reconstruct the pitch of a tone when presented with a reference tone. Only about 0.01% of the general population (Bachem, 1955; Profita and Bidder, 1988; Takeuchi and Hulse, 1993) and about 4–15% of musicians (Baharloo et al., 1998; Gregersen et al., 1999, 2001; Leite et al., 2016) possess the unique ability to recognize the pitch class of a tone or to produce a specific pitch without the aid of a reference tone. This ability is referred to as absolute pitch (AP; Deutsch, 2013).

Pitch identification in AP is fast and effortless (Miyazaki, 1990; Deutsch, 2013), and is even presumed to be automatic (Levitin and Rogers, 2005). The extent of this automaticity has been studied primarily using auditory Stroop tasks (Miyazaki, 2004; Itoh et al., 2005; Hsieh and Saberi, 2008; Akiva-Kabiri and Henik, 2012; Schulze et al., 2013). Originally, the Stroop effect (Stroop, 1935) describes the phenomenon that naming the ink color of a semantically incongruent color word (e.g., the word "RED" printed in the color blue) is slower than naming the ink color of solid-color squares. By contrast, the latency for reading the words printed in color is not reliably increased compared to the same words printed in black. The more automatic process (i.e., reading) impedes the less automatic process (i.e., color naming) but not vice versa. Stroop tasks (for an overview, see MacLeod, 1991) use this asymmetrical effect to assess the ability to inhibit cognitive interference. In AP research, auditory analogs of the Stroop task typically consist of trials where the pitch of a tone is either congruent or incongruent with the sung tone label (integrated stimuli; e.g., Itoh et al., 2005) or a visual note presented simultaneously (non-integrated stimuli; e.g., Akiva-Kabiri and Henik, 2012). In incongruent trials, AP musicians consistently show increased response times for label/note naming compared to congruent trials. Pitch labeling, on the other hand, seems to be less affected by incongruence (Akiva-Kabiri and Henik, 2012). Furthermore, studies have shown that AP musicians perform worse than non-AP musicians in interval identification when given an out-of-tune context (Miyazaki, 1992, 1993) and in recognition of transposed atonal melodies (Miyazaki and Rakowski, 2002). As Dooley and Deutsch (2010, 2011) pointed out, these findings may reflect Stroop-like interference effects rather than a general disadvantage in relative-pitch tasks. Taken together, this suggests that the pitch-labeling process in AP is highly automatic and difficult to suppress.

At a more general level, several neurophysiological studies reported that AP musicians showed increased activity in different brain areas (e.g., in the auditory cortex, the planum temporale, the inferior frontal gyrus, and the DLPFC) during acoustic stimulation compared to non-AP musicians even when not instructed to perform pitch labeling (Zatorre et al., 1998; Ohnishi et al., 2001; Wu et al., 2008; Wengenroth et al., 2014; Burkhard et al., 2019; Leipold et al., 2019a). These findings indicate that tone processing in AP musicians is generally altered and that at least some AP-specific processes might be automatically triggered by musical tones. This assumption received further support from a recent decoding study that found a greater representational similarity in electrophysiological activity between a pure listening task and a labeling task in AP musicians compared to non-AP musicians (Leipold et al., 2019b).

The current study aimed to further explore the automaticity and suppressibility of pitch labeling in AP by examining both electrophysiological and behavioral correlates of another prominent psychological paradigm: the Go/Nogo task. Like Stroop tasks, Go/Nogo tasks are widely used to evaluate executive functions, particularly the capacity for inhibitory control. Typically, participants are instructed to press a button as quickly as possible whenever a target stimulus appears within a series of stimuli (Go) and to withhold the button press when a non-target stimulus appears (Nogo). A prominent advantage of Go/Nogo tasks is that the cognitive processes can be evaluated by both behavioral and well-established electrophysiological measures. The main behavioral measures are failures to inhibit a prepared motor response in Nogo trials (called commission errors or false alarms), failures to respond to the target in Go trials (called omission errors or misses), and response times in Go trials. The main electrophysiological measures are two event-related potential (ERP) components associated with reactive cognitive control: the Nogo-N2 and the Nogo-P3. The Nogo-N2, a negative deflection at frontal-midline sites, peaks around 200–400 ms after stimulus onset. The Nogo-P3, the subsequent frontocentral positive shift, is at its maximum about 300–600 ms after stimulus onset (e.g., Pfefferbaum et al., 1985; Pfefferbaum and Ford, 1988; Jodo and Kayama, 1992; Falkenstein et al., 1995, 1999; Bokura et al., 2001; Folstein and Van Petten, 2008; Gajewski and Falkenstein, 2013). Both the N2 and the P3 are usually evaluated by subtracting the Go ERP from the Nogo ERP (Nogo minus Go). In the following, we will refer to the N2 and P3 of the resulting difference wave as N2d and P3d. The exact cognitive subprocesses of response inhibition reflected by the N2 and P3 have been controversially discussed (for a review, see Huster et al., 2013). While some studies associated the N2 with pre-motor inhibitory processes (Jodo and Kayama, 1992; Falkenstein et al., 1999; Bokura et al., 2001; Gajewski and Falkenstein, 2013), other research indicates that the N2 reflects response activation (Bruin et al., 2001) or conflict monitoring (Nieuwenhuis et al., 2003; Donkers and Van Boxtel, 2004; Yeung et al., 2004; Enriquez-Geppert et al., 2010; Kropotov et al., 2017). The P3 has been suggested to mirror inhibitory processes or the evaluation of successful inhibition (Bokura et al., 2001; Bruin and Wijers, 2002; Donkers and Van Boxtel, 2004; Smith et al., 2008; Enriquez-Geppert et al., 2010; Albert et al., 2013; Kropotov et al., 2017).

In the current study, 54 AP and 51 non-AP musicians completed a cued (two-stimulus) Go/Nogo task with acoustic stimuli (i.e., piano tones and environmental sounds). The cue (i.e., a piano tone) was used to establish a prepotent tendency to respond. A button press was required whenever two identical piano tones were presented in succession (Go condition). In trials where two non-identical piano tones were presented, the button press had to be withheld (Nogo condition). Two variations of the Nogo condition were included. In the first Nogo condition, the two presented piano tones differed by at least one semitone (100–700 cents). In the second Nogo condition, the

two piano tones differed by only a quarter semitone (25 cents). Using these two Nogo conditions allowed us to study different aspects of pitch processing in AP: (1) inhibition of a possibly stronger neurophysiological activation induced by tones; and (2) suppressibility of pitch labeling. As described above, acoustic stimulation elicits strong neurophysiological activation in AP musicians. This, in turn, might influence subsequent cognitive processes and their respective neurophysiological correlates. The first Nogo condition was used to test whether the generally altered tone processing affects the subsequent inhibitory processes in AP musicians. The second Nogo condition, on the other hand, might generate a Stroop-like effect: the two piano tones, although slightly different in tone frequency, belonged to the same pitch category and should, therefore, evoke the same pitch label in AP musicians. It has been shown before that AP musicians categorize mistuned tones in their nominal categories (e.g., a mistuned C will still be identified as C; Levitin and Rogers, 2005). If pitch labeling is difficult to suppress, AP musicians are expected to show some signs of increased inhibitory load due to the conflicting information, such as more commission errors and/or larger N2d/P3d amplitudes than non-AP musicians. Also, it has been suggested that AP musicians may have an aversion towards mistuned tones (Levitin and Rogers, 2005; Rogenmoser et al., 2020). This could increase the inhibitory load even further.

Finally, we also included a behavioral audio-visual Stroop task to confirm the presence of an incongruence effect as reported in previous studies in our sample of AP participants.

MATERIALS AND METHODS

Participants

All 105 participants were recruited within a larger research project investigating the neural correlates of AP (Greber et al., 2018, 2020; Brauchli et al., 2019, 2020; Burkhard et al., 2019, 2020; Leipold et al., 2019a,b,c) and were professional musicians, music students, or highly-trained amateur musicians. In total, 54 musicians with AP and 51 musicians without AP participated in this study. The age of the participants ranged from 18 to 44 years. Participants were assigned to one of the two groups based on self-report in the initial online application form. This assignment was validated by an online pitch-labeling task (described below). If someone had self-identified as AP possessor but scored around or below the chance level of 8.3% in the pitch-labeling task, they were not invited to participate in the study. If someone had self-identified as non-AP possessor, which was confirmed again in the laboratory, and nonetheless achieved high scores in the pitch-labeling task, they were neither excluded from the study nor reassigned to the AP group.

Before being invited to the electroencephalography (EEG) recording, participants also filled out an online questionnaire assessing demographical information and musical experience. Based on these data, the two groups were matched for sex, age, handedness, age of onset of musical training, and cumulative hours of musical training over the lifespan.

None of the participants reported any neurological, severe psychiatric, or audiological disorders. We confirmed normal hearing thresholds in all participants using pure-tone audiometry (MAICO ST 20, MAICO Diagnostic, GmBh, Berlin) and validated self-reported handedness using a German translation of the Annett Handedness Questionnaire (Annett, 1970). Crystallized intelligence was evaluated with the Mehrfachwahl-Wortschatz-Intelligenztest (MWT-B; Lehrl, 2005), and fluid intelligence was evaluated with the Kurztest für Allgemeine Basisgrössen der Informationsverarbeitung (KAI: Lehrl and Fischer, 1992). Musical aptitude was estimated using the Advanced Measures of Music Audiation (AMMA; Gordon, 1989). The AMMA consists of 30 pairs of piano melodies. Participants are asked to decide whether the two melodies are identical, different in rhythmical patterns, or different in tonal patterns. The test results in a rhythmical score, a tonal score, and a total score (equals the sum of rhythmical and tonal score). Participant characteristics for the two groups are given in **Table 1**.

TABLE 1 | Participant characteristics.

	Absolute Pitch Musicians (n = 54)	Non-Absolute Pitch Musicians (n = 51)
Sex		
Female	27	24
Male	27	27
Age (years)	26.67 (5.49)	25.37 (4.49)
Handedness		
Right-handed	47	46
Left-handed	4	4
Both-handed	3	1
Intelligence (MWT-B)[a]	27.69 (5.10)	29.10 (4.64)
Intelligence (KAI)[a]	123.41 (32.16)	132.19 (26.16)
Age of Onset of Musical Training (years)	5.93 (2.39)	6.49 (2.44)
Lifetime Cumulative Training (hours)[b]	1.66 (1.22)	1.35 (0.96)
Musical Aptitude (AMMA)[a]—total	66.11 (6.31)	63.35 (6.86)
Musical Aptitude (AMMA)[a]—total	32.33 (3.75)	30.45 (4.13)
Musical Aptitude (AMMA)[a]—rhythmical	33.78 (2.83)	32.90 (3.03)
Pitch-labeling Test (%)	76.41 (19.55)	24.04 (18.92)

Continuous measures are given as mean (standard deviations in parentheses). MWT-B, Mehrfachwahl-Wortschatz-Intelligenztest; AMMA, Advanced Measures of Music Audiation. [a]Raw scores. [b]Units are given in 1×10^4.

The study was approved by the ethics committee of the canton of Zurich[1] and was conducted in accordance with the Declaration of Helsinki. All participants provided written informed consent and received payment for their participation.

Pitch-Labeling Task

As described above, participants completed an online pitch-labeling task at home before being invited to the laboratory. During the task (adapted from Oechslin et al., 2010), participants were instructed to identify both the pitch chroma (class, e.g., C) and the pitch height (octave, e.g., 4) of 108 pure tones. Tones ranged from C3 to B5 (tuning: A4 = 440 Hz) and had a duration of 500 ms. Immediately before and after each tone, 2,000 ms of Brownian noise were presented. In total, each tone was presented three times in a pseudorandomized order, ensuring that tones were not repeated in consecutive trials. Participants responded by selecting a label from a list of all possible labels (C3 to B5) within a maximal trial duration of 15,000 ms. Following the same scoring procedure as the other studies within the AP project (Greber et al., 2018, 2020; Brauchli et al., 2019, 2020; Burkhard et al., 2019, 2020; Leipold et al., 2019a,b,c), we quantified pitch-labeling ability as the percentage of correctly identified pitch classes without considering octave errors (Deutsch, 2013). We did not assign full or partial points to semitone errors. Accordingly, the chance level was at 8.3%.

Auditory-Visual Stroop Task

An auditory-visual Stroop task (Stroop, 1935) was administered in the laboratory to assess the automaticity of pitch labeling (Allport et al., 1994; Itoh et al., 2005; Akiva-Kabiri and Henik, 2012; Schulze et al., 2013). This task has already been reported in another study for the same sample within the larger project on AP (Leipold et al., 2019b). During the task, auditory and visual stimuli were presented simultaneously. Both auditory and visual stimuli corresponded to C4, D4, E4, F4, and G4. The five auditory stimuli were pure tones with a duration of 500 ms (10 ms linear fade-in; 50 ms linear fade-out), created using Audacity (version 2.1.2)[2]. The visual stimuli consisted of the matching musical notations as quarter notes in treble clef. During the simultaneous presentation, the label of the tone and the name of the musical notation were either congruent or incongruent. Participants were asked to identify the visually presented musical notations as fast and accurately as possible by button press (keys labeled as C, D, E, F, or G) and to ignore the acoustically presented tones. If pitch labeling in AP musicians is automatic and difficult to suppress, AP musicians are expected to experience more cognitive interference in incongruent trials than non-AP musicians. This would be reflected by greater differences in response time between congruent and incongruent trials in AP musicians.

Response times were averaged separately for each participant and condition. Incorrect trials and response times that deviated by more than two standard deviations from the corresponding participant-and-condition-specific mean were excluded from the analysis. For each participant, we subtracted the mean response time of the congruent trials from the mean response time of the incongruent trials to quantify the Stroop effect. These differences in response times between congruent and incongruent trials were subjected to statistical group comparison.

EEG Experiment: Auditory Go/Nogo Continuous Performance Task

During EEG recording, participants performed an auditory continuous performance task (ACPT) requiring Go/Nogo decisions. The auditory stimuli consisted of piano tones and environmental sounds. We used piano tones instead of pure tones for this task because the pitches of piano tones are usually easier to identify than those of piano tones (Miyazaki, 1989; Van Hedger and Nusbaum, 2018; Gruhn et al., 2019). Easy recognition of the pitch class was essential so that conflicting information regarding the sameness of the stimuli could potentially arise in the second Nogo condition.

Initially, five white-key piano tones (C4, D4, E4, F4, and G4) and 10 environmental sounds (e.g., water splashes, knocking on wood) were recorded. These auditory stimuli were then preprocessed using the Audacity software (Version 2.1.2)[2]. They were all shortened to 500 ms and normalized. A linear fade-in and a linear fade-out were applied to the first and last 100 ms respectively. Additional mistuned piano tones were generated by shifting the pitch of each of the originally recorded piano tones $\frac{1}{4}$ semitone (=25 cents) to sharp and to flat. In total, five in-tune piano tones, 10 mistuned piano tones, and 10 environmental sounds were used in the experiment.

The ACPT task consisted of 400 trials. Before starting the task, participants were asked to perform a few practice trials to check whether they had understood the task instruction. After 200 trials, participants were allowed to take a short break.

In each trial, two of the auditory stimuli were presented one after the other *via* Bose Companion 2 Series III external speakers (Bose Corporation, Framingham, MA, USA) at a sound pressure of approximately 75 dB using the ERPrec software (Version 2.0.x, Bee Medic GmbH, Germany). Trials lasted 3,800 ms with an interstimulus interval of 1,000 ms. The first stimulus was presented 300 ms after the start of the trial for a duration of 500 ms. After 500-ms presentation of the second stimulus, participants were given 1,500 ms to indicate a response. A black fixation cross on a white background was presented on the screen during the entire task.

There were four different trial categories: Go trials, Nogo trials with in-tune tones ($Nogo_{it}$), Nogo trials with mistuned tones ($Nogo_{mt}$), and Ignore trials (compare **Figure 1**). All four trial categories were presented in randomized order and with equal probability (100 trials each). Participants were instructed to press the left mouse button with the right index finger as quickly and as accurately as possible whenever two identical piano tones were presented successively. The first stimulus was either an in-tune piano tone or an environmental sound. Thus, a piano tone as the first stimulus served as a cue for a potential button press, whereas an environmental sound indicated that no action was necessary (Ignore trial). In Go trials, the first piano

[1] http://www.kek.zh.ch
[2] http://www.audacityteam.org/

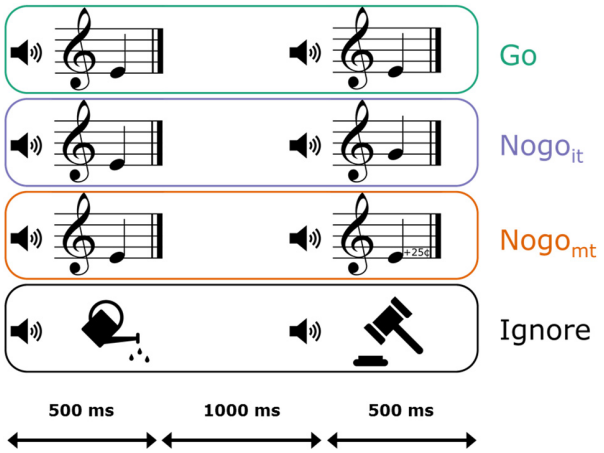

FIGURE 1 | Graphical representation of the four trial categories in the auditory continuous performance task (ACPT). Participants were instructed to press a mouse button as fast and accurately as possible when a piano tone was followed by an identical piano tone (Go, depicted in green). When the second piano tone was a non-identical in-tune piano tone (Nogo$_{it}$, depicted in violet) or a mistuned variant of the first piano tone (Nogo$_{mt}$, depicted in orange; 25-cents deviation of the first stimulus), participants had to inhibit the prepared response. When the first stimulus was an environmental noise instead of a piano tone, no response had to be prepared (Ignore, depicted in black). Stimuli had a duration of 500 ms, and the interstimulus interval had a duration of 1,000 ms.

tone was followed by an identical piano tone, thus requiring a button press. In Nogo$_{it}$ trials, the second stimulus was also an in-tune piano tone but belonging to a different pitch class (e.g., E4 followed by G4). In Nogo$_{mt}$ trials, the second stimulus was one of the slightly mistuned variants of the first stimulus (e.g., E4 followed by the 25-cents-sharp deviation of E4). In both Nogo$_{it}$ and Nogo$_{mt}$ trials, participants had to withhold pressing the button. In Nogo$_{mt}$ trials, pitch labels of the two successive tones were identical, but pitch height was not. Thus, in the case of automatic pitch labeling, these trials contain conflicting information about the sameness of the two stimuli. If potential automatic labeling interferes with the task demands, AP musicians should demonstrate signs of a higher inhibitory load (i.e., larger N2d$_{mt}$ or P3d$_{mt}$ amplitudes, and/or higher error rates) compared to non-AP musicians in Nogo$_{mt}$ trials.

Performance in the ACPT task was quantified as mean response time, number of omission errors, and number of commission errors. Response times were analyzed for correct Go trials and were measured as the time elapsed between the onset of the second stimulus and button press. Response times shorter than 200 ms and longer than 1,500 ms were not included in the average. Failures to respond in Go trials were counted as omission errors. Failures to inhibit a button press in Nogo$_{it}$ and Nogo$_{mt}$ trials were counted as commission errors. Trials in which a button press occurred between the first and the second stimulus were excluded from the behavioral analysis.

EEG Recording and Preprocessing

For the EEG recording, participants were seated in an electrically shielded room and were instructed to fixate their gaze on a black cross on a white screen during the task. Before the experimental task, 3 min of eyes-open and 3 min of eyes-closed resting state were acquired. Continuous EEG was recorded from 31 scalp sites using an electrode cap (Comby EEG Cap, Pamel, Croatia), a Neuroamp®x39 amplifier (Bee Medic GmbH, Germany), and the ERPrec recording software (Version 2.0.x, Bee Medic GmbH, Germany). The silver/silver chloride electrodes were placed according to a subset of the 10/10 system (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T3, C3, Cz, C4, T4, TP7, CP3, CPz, CP4, TP8, T5, P3, Pz, P4, T6, O1, Oz, O2) and referenced to linked earlobes. Impedances of all electrodes were kept below 10 kΩ using an abrasive, electrically conductive gel (OneStep EEG-Gel, H + H Medizinprodukt GbR, Germany). The sampling rate was 500 Hz and no online filters were applied. After recording, data was converted to EDF+ using the xdf2eeg file converter implemented in the ERPrec software. During file conversion, a high-pass filter (Butterworth, 1st order) of 0.16 Hz and a fixed range scaling factor were applied to the EEG signal.

The converted data was subsequently preprocessed using the BrainVision Analyzer software package (Version 2.1, BrainProducts, Germany)[3]. First, the data was filtered with a bandpass filter (Butterworth, 8th order) of 1–30 Hz and a notch filter of 50 Hz. Next, eye movement artifacts were corrected using a restricted infomax independent component analysis (ICA; Jung et al., 2000). Noisy channels were excluded from the ICA and interpolated after ICA correction. Remaining artifacts were marked using an automatic raw data inspection with the following exclusion criteria: amplitude gradient >50 μV/ms, amplitude difference >100 μV within an interval of 200 ms, amplitude <−100 μV, amplitude >+100 μV, and activity <0.5 μV within an interval of 100 ms.

Then, ERPs evoked by the second stimulus were computed separately for the three cued conditions (Go, Nogo$_{it}$, and Nogo$_{mt}$) and for each participant. The EEG signal was divided into artifact-free segments of 1,100 ms (−100 to +1,000 ms from the onset of the second stimulus), and baseline correction (−100 to 0 from the onset of the second stimulus) was applied. Only trials with a correct response (button press in Go; no button press in Nogo$_{it}$ and Nogo$_{mt}$) were included in the ERP averages. Grand and group averages of the ERPs at Fz, Cz, and Pz are shown in **Figure 2**. **Supplementary Figure 1** shows the grand averages of the ERPs at all 31 electrodes. **Supplementary Figures 2, 3, 4** show the ERPs at all 31 electrodes separately for the two groups.

Two difference waves were computed by subtracting the participant-specific ERP evoked in the Go condition from the participant-specific ERPs evoked in the two inhibition conditions (Nogo$_{it}$ minus Go and Nogo$_{mt}$ minus Go). The N2 and P3 ERP components on the difference waves (N2d and P3d) were quantified as mean amplitudes at the three midline electrodes Fz, Cz, and Pz. Compared to peak amplitudes, mean amplitudes are more robust, less affected by latency variability between trials, and not biased by the noise level and the number of trials

[3]https://www.brainproducts.com/

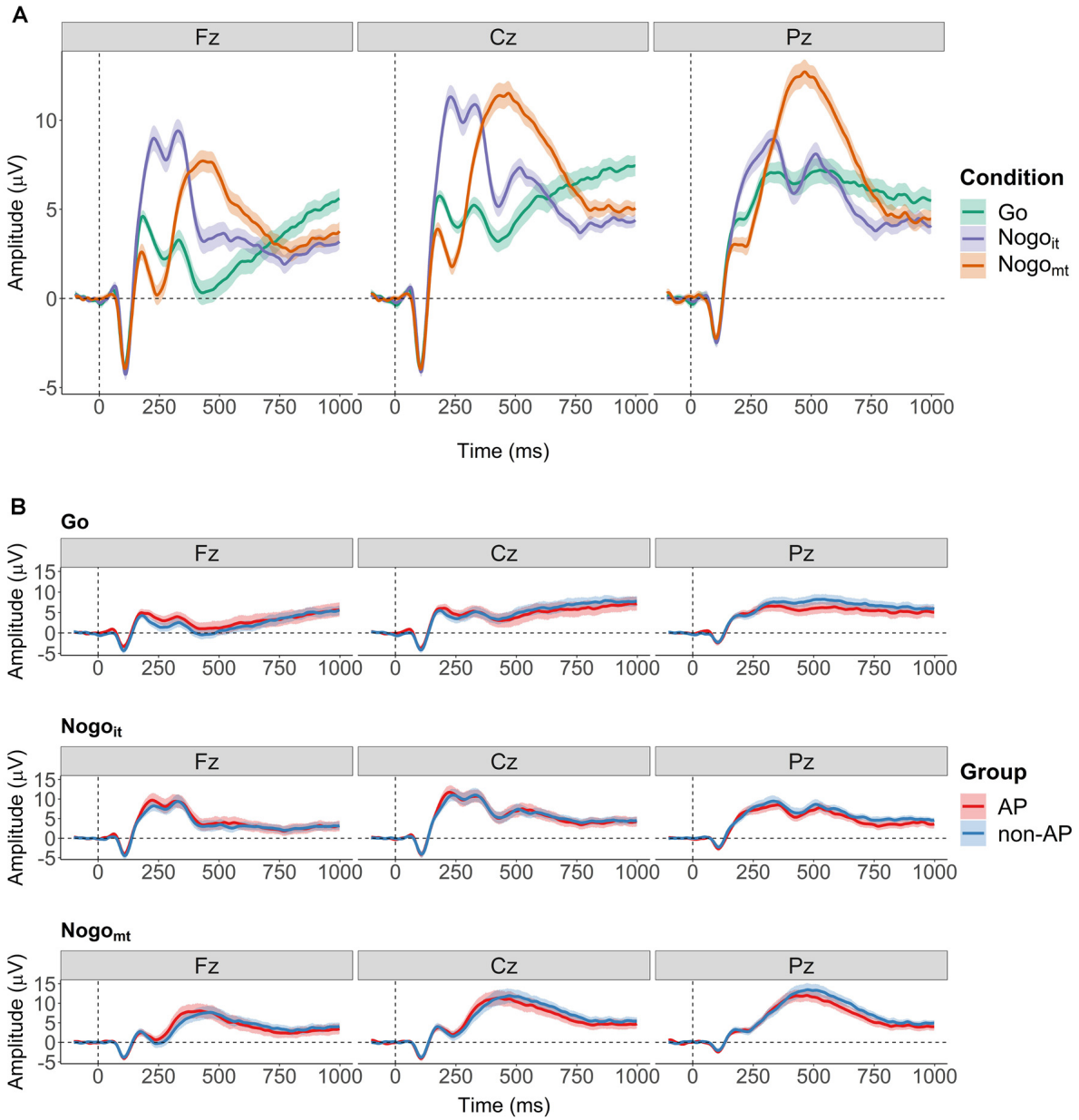

FIGURE 2 | Grand averages of the event-related potentials (ERPs) evoked by the second stimulus. **(A)** Grand averages over all participants for the three cued conditions (Go in green, Nogo$_{it}$ in violet, and Nogo$_{mt}$ in orange). Shaded areas depict the 95% within-subject confidence interval. **(B)** Grand averages computed separately for AP musicians (red) and non-AP musicians (blue). Shaded areas depict the 95% between-subject confidence interval.

(Clayson et al., 2013; Luck, 2014). The definition of the time windows was based on the grand averages of the difference waves over all participants at electrode Cz (compare **Figure 3**). Because the onset and expansion of N2d and P3d differed between the two conditions, separate time windows were selected for Nogo$_{it}$-Go and Nogo$_{mt}$-Go. From now on, ERP components obtained from the difference wave between Nogo$_{it}$ and Go will be referred to as N2d$_{it}$ and P3d$_{it}$. ERP components obtained from the difference wave between Nogo$_{mt}$ and Go will be referred to as N2d$_{mt}$ and P3d$_{mt}$. Mean amplitudes were computed for N2d$_{it}$ between 100 and 140 ms, for P3d$_{it}$ between 180 and 420 ms, for N2d$_{mt}$ between 150 and 270 ms, and for P3d$_{mt}$ between 320 and 660 ms after stimulus onset. Time windows and topographies of the components are shown in **Figures 3A,B**, respectively. Visualizations of topographies and ERPs were created using functions from the R package EEGutils (Craddock, 2018). **Supplementary Figure 5** shows the difference waves at all 31 electrodes averaged across all participants. **Supplementary Figures 6, 7** show the difference waves at all 31 electrodes separately for the two groups.

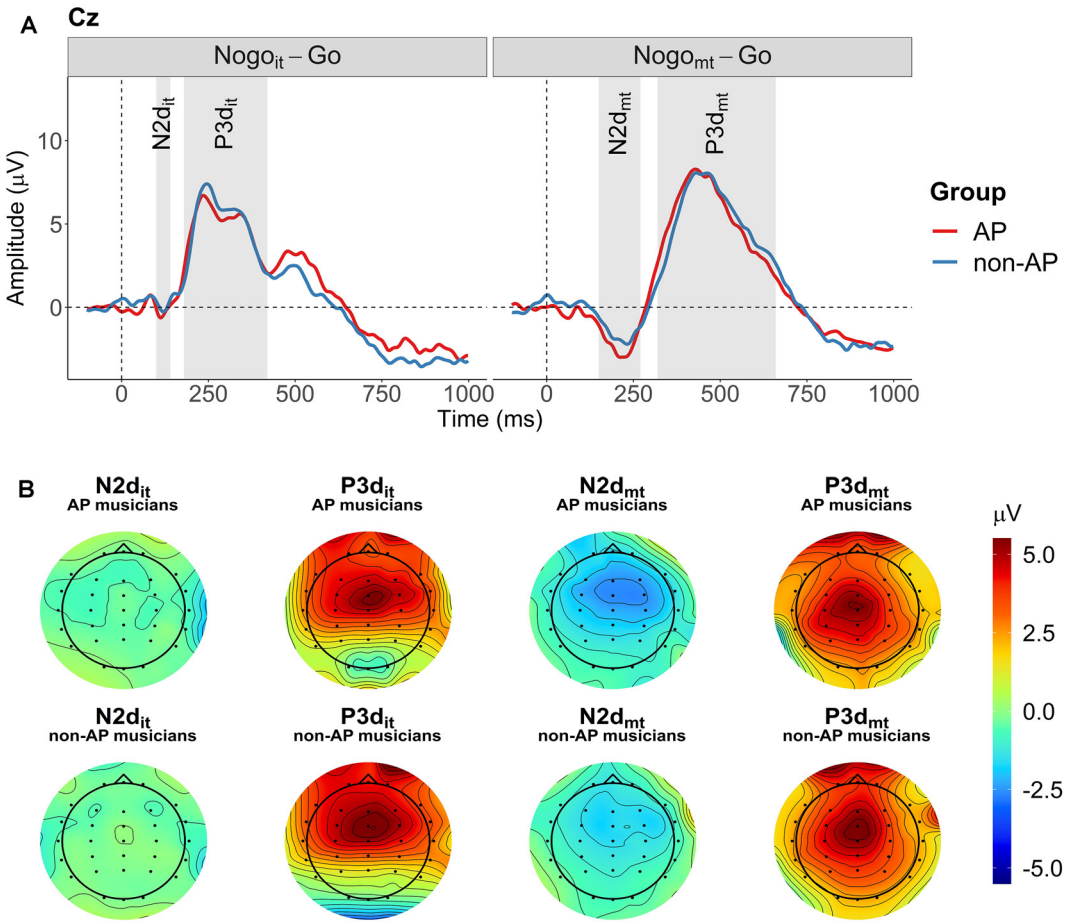

FIGURE 3 | Grand averages and topographies of the difference waves (Nogo$_{it}$ minus Go, Nogo$_{mt}$ minus Go). **(A)** Grand averages of the two difference waves are shown separately for the two groups at electrode Cz (red: AP musicians, blue: non-AP musicians). Time windows used for the computation of mean amplitudes are indicated by the gray-shaded areas. **(B)** Topographies for the four ERP components of interest (N2d$_{it}$, P3d$_{it}$, N2d$_{mt}$, and P3d$_{mt}$) are shown separately for AP and non-AP musicians.

Mean amplitudes and time series of the difference wave ERPs at electrodes Fz, Cz, and Pz were exported for statistical analyses.

Statistical Analysis

All statistical analyses were performed using R (version 3.4.3[4]; R Core Team, 2017). The significance level was set to $\alpha = 0.05$ for all statistical analyses unless stated otherwise. We compared the participant characteristics, the AMMA scores (rhythmical, tonal, and total), the Stroop effect, and the pitch-labeling score between the two groups using two-tailed Welch's *t*-tests. Additionally, we computed Pearson correlations between the pitch-labeling scores and the Stroop effect across all participants as well as within each group.

Group differences in the performance measures of the ACPT (i.e., mean response times, omission errors, commission errors in Nogo$_{it}$ trials, and commission errors in Nogo$_{mt}$ trials) were also evaluated using Welch's *t*-tests. Effect sizes for *t*-tests are given as Cohen's *d* (Cohen, 1988).

To analyze group differences in the EEG data, we used two different approaches. First, we performed a traditional ERP-component analysis: we compared the N2d and P3d mean amplitudes between the two groups separately for the Nogo$_{it}$-Go and the Nogo$_{mt}$-Go condition. For each component (N2d$_{it}$, P3d$_{it}$, N2d$_{mt}$, P3d$_{mt}$), we computed a 2 × 3 ANOVA with between-subject factor Group (AP and non-AP) and within-subject factor Electrode Site (Fz, Cz, Pz) using the R package *ez* (version 4.4.0[5]; Lawrence, 2016). *P*-values and degrees of freedom were adjusted with the Greenhouse-Geisser correction for nonsphericity when appropriate. Effect sizes for the main effects and interactions are given as generalized eta-squared (η^2_G, Bakeman, 2005). To quantify the relative evidence of the alternative hypothesis (H1) and the null hypothesis (H0), we additionally report Bayes factors for the mean amplitudes. Bayes

[4]https://www.r-project.org

[5]https://cran.r-project.org/web/packages/ez/index.html

factors compare the (marginal) likelihood of the data between two hypotheses (i.e., H1 and H0). Contrary to frequentist statistics, this allows for conclusions about the evidence in support of H0 (Dienes, 2011, 2014). The likelihood ratio expressed by a Bayes factor can be interpreted as follows: A BF_{10} of 5 (or the inverse $\frac{1}{BF_{10}} = BF_{01}$ of 0.2) indicates that the observed data is five times more likely under H1 than under H0. To make the interpretation more straightforward for the reader, we report BF_{10} when the relative evidence is in favor of H1, and BF_{01} when the relative evidence is in favor of H0.

We computed the Bayes factors using the R package *BayesFactor* (version 0.9.12-4.2[6]; Morey et al., 2018). We used the default settings implemented in the *BayesFactor* package for the number of iterations (n = 10,000) and for the prior scale parameter (r = 0.707 for Bayesian t-tests; r = 0.5 for Bayesian ANOVAs). To assess the two main effects of the Bayesian ANOVAs (i.e., group and electrode), the model with one factor (e.g., group + subject) was compared to the model with both factors (e.g., group + electrode + subject). For the interaction effect, the full model (group + electrode + group * electrode + subject) was compared to the model without the interaction effect (group + electrode + subject).

Second, we adopted a more data-driven approach to analyze the difference waves. Using cluster-based permutation tests implemented in the R package *permuco* (version 1.0.2[7] ; Frossard and Renaud, 2019), we performed a 2 × 2 ANOVA with between-subject factor Group (AP and non-AP) and within-subject factor Condition ($Nogo_{it}$-Go and $Nogo_{mt}$-Go) at each time point after stimulus onset (0 to 1,000 ms). This analysis was conducted separately for each of the three electrodes (Fz, Cz, and Pz). To control for multiple comparisons over time-points, threshold-free cluster enhancement (TFCE: Smith and Nichols, 2009; Mensen and Khatami, 2013) was combined with non-parametric maximum permutation statistics. The TFCE procedure incorporates neighborhood information (i.e., time points close to each other tend to correlate) and does not require an arbitrary cluster-forming threshold. The same procedure was repeated 5,000 times using randomly permuted datasets of the original dataset. From each permutation step, the maximal TFCE score was obtained to form an empirical null distribution, to which the TFCE scores from the original datasets were compared.

RESULTS

Demographic and Behavioral Data

The two groups were comparable in age ($t_{(100.97)} = 1.33$, $p = 0.19$, $d = 0.26$), crystallized intelligence (MWT-B: $t_{(102.86)} = -1.49$, $p = 0.14$, $d = 0.29$), fluid intelligence (KAI: $t_{(100.82)} = -1.54$, $p = 0.13$, $d = 0.30$), age of onset of musical training ($t_{(102.42)} = -1.20$, $p = 0.23$, $d = 0.23$), and cumulative musical training hours over the lifespan ($t_{(99.71)} = 1.43$, $p = 0.16$, $d = 0.28$). AP musicians scored slightly higher in the AMMA total score ($t_{(100.99)} = 2.14$, $p = 0.035$, $d = 0.42$). Analyses of the subtests revealed that this effect was driven by higher AMMA tonal scores in AP musicians ($t_{(100.61)} = 2.44$, $p = 0.016$, $d = 0.48$). In the AMMA rhythmical score, AP and non-AP musicians were comparable ($t_{(101.38)} = 1.53$, $p = 0.13$, $d = 0.30$). In the pitch-labeling task, AP musicians performed considerably better than non-AP musicians ($t_{(102.93)} = 13.95$, $p < 0.001$, $d = 2.72$; see **Figure 4A**). In the auditory-visual Stroop task, AP musicians showed a larger incongruence effect than non-AP musicians ($t_{(102.65)} = 2.78$, $p = 0.007$, $d = 0.54$; see **Figure 4B**), indicating difficulties to suppress pitch labeling in this task. Across the whole sample, pitch-labeling scores were positively correlated with the size of the incongruence effect in the auditory-visual Stroop task ($r = 0.24$, $p = 0.015$). Within the groups, there was no evidence for a relationship between pitch-labeling scores and the size of the Stroop effect (AP: $r = -0.12$, $p = 0.37$; RP: $r = 0.22$, $p = 0.12$).

ACPT Performance Data

Musicians with AP and musicians without AP showed comparable error rates for omission errors ($t_{(92.40)} = 0.70$, $p = 0.48$, $d = 0.14$), commission errors in $Nogo_{it}$ trials (mean AP musicians = 0.19, SD AP musicians = 0.44, mean non-AP musicians = 0.22, SD non-AP musicians = 0.54; $t_{(96.23)} = -0.32$, $p = 0.75$, $d = 0.06$), and commission errors in $Nogo_{mt}$ trials (mean AP musicians = 1.76, SD AP musicians = 4.83, mean non-AP musicians = 1.96, SD non-AP musicians = 2.69; $t_{(83.95)} = -0.27$, $p = 0.79$, $d = 0.05$). Response times in Go trials were on average slightly longer in AP musicians (mean response time = 781.37 ms, SD = 188.27 ms) than in non-AP musicians (mean response time = 719.94 ms, SD = 159.40 ms), but the difference was not statistically significant ($t_{(101.81)} = -1.81$, $p = 0.073$, $d = 0.35$). Performance measures are shown in **Figures 5A,B**.

EEG Data: N2d and P3d Mean Amplitudes

Mean amplitudes of the ERP components are shown in **Figure 6**. The two-way ANOVA of the $N2d_{it}$ amplitudes did not reveal a main effect of Group ($F_{(1.103)} = 0.82$, $p = 0.37$, $\eta^2_G = 0.006$, $BF_{01} = 2.32$), a main effect of Electrode ($F_{(1.33,137.16)} = 2.16$, $p = 0.14$, $\eta^2_G = 0.004$, $BF_{01} = 4.03$), or an interaction effect ($F_{(1.33,137.16)} = 0.12$, $p = 0.80$, $\eta^2_G < 0.001$, $BF_{01} = 14.10$). The analysis of the $P3d_{it}$ amplitudes also revealed no main effect of Group ($F_{(1.103)} = 0.24$, $p = 0.62$, $\eta^2_G = 0.002$, $BF_{01} = 2.68$) and no Group × Electrode interaction ($F_{(1.41,145.26)} = 0.77$, $p = 0.42$, $\eta^2_G = 0.001$, $BF_{01} = 8.94$), but did reveal a main effect of Electrode ($F_{(1.41,145.26)} = 145.92$, $p < 0.001$, $\eta^2_G = 0.21$, $BF_{10} = 1.04 * 10^{37}$). According to pairwise comparisons, $P3d_{it}$ amplitudes were smaller at Pz (mean = 1.49 μV, SD = 2.84 μV) than at Fz (mean = 5.06 μV, SD = 3.49 μV, $t_{(104)} = 11.60$, $p < 0.001$, $d = 1.13$, $BF_{10} = 2.62 * 10^{17}$) and at Cz (mean = 5.03 μV, SD = 3.43 μV, $t_{(104)} = 18.89$, $p < 0.001$, $d = 1.84$, $BF_{10} = 1.23 * 10^{32}$).

The two-way ANOVA of the $N2d_{mt}$ amplitudes similarly revealed a main effect of Electrode ($F_{(1.32,135.71)} = 27.50$, $p < 0.001$, $\eta^2_G = 0.035$, $BF_{10} = 2.25 * 10^8$). Again pairwise comparisons showed that amplitudes were less pronounced at electrode Pz (mean = −1.25 μV, SD = 1.93 μV) than at electrode Fz (mean = −2.12 μV, SD = 2.12 μV, $t_{(104)} = -5.25$, $p < 0.001$, $d = 0.51$, $BF_{10} = 1.62 * 10^4$) and electrode Cz (mean = −1.96 μV, SD = 2.02 μV, $t_{(104)} = -7.05$, $p < 0.001$, $d = 0.69$, $BF_{10} = 4.62$

[6]https://cran.r-project.org/web/packages/BayesFactor/index.html
[7]https://cran.r-project.org/web/packages/permuco/index.html

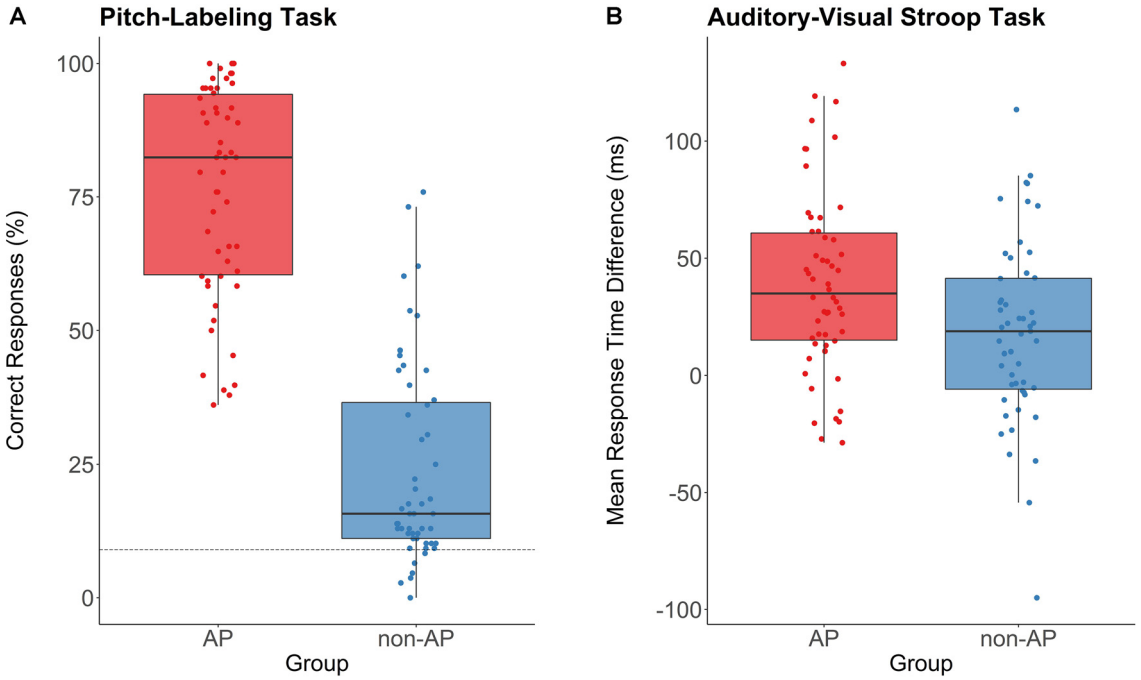

FIGURE 4 | Performance in the pitch-labeling task and the auditory-visual Stroop task for AP musicians (n = 54, depicted in red) and non-AP musicians (n = 51, depicted in blue). **(A)** AP musicians showed a substantially better pitch-labeling ability. The dashed line represents the chance level of 8.3%. **(B)** The incongruence effect (response time difference between congruent and incongruent trials) in the Stroop task was more pronounced in AP musicians than in non-AP musicians. This indicates that the pitch labeling was difficult to suppress for our sample of AP musicians.

$^{*}10^{7}$). We found no main effect of Group ($F_{(1.103)}$ = 2.87, p = 0.093, η^2_G = 0.024, BF_{01} = 1.01) nor an interaction effect ($F_{(1.32,135.71)}$ = 2.93, p = 0.078, η^2_G = 0.004, BF_{01} = 1.20) for the $N2d_{mt}$ amplitudes.

The evaluation of the $P3d_{mt}$ amplitudes did not reveal a main effect of Group ($F_{(1.103)}$ = 0.05, p = 0.82, η^2_G < 0.001, BF_{01} = 2.52), but did reveal a main effect of Electrode ($F_{(1.50,154.31)}$ = 21.89, p < 0.001, η^2_G = 0.022, BF_{10} = 1.89 $^{*}10^{6}$) and a Group × Electrode interaction ($F_{(1.50,154.31)}$ = 6.22, p = 0.006, η^2_G = 0.006, BF_{10} = 12.69). The *post hoc* t-tests comparing the $P3d_{mt}$ amplitudes between the two Groups at each electrode provided no evidence for a difference between AP and non-AP musicians at any of the three electrodes (Fz: $t_{(100)} = -1.40$, p = 0.16, d = 0.27, BF_{01} = 2.01; Cz: $t_{(102.9)}$ = 0.006, p = 0.995, d = 0.001, BF_{01} = 4.85; Pz: $t_{(101.9)}$ = 0.65, p = 0.52, d = 0.13, BF_{01} = 4.01).

EEG Data: Cluster-Based Permutation Test

The non-parametric cluster-based permutation tests indicated an effect of condition at all three analyzed electrode sites (p = 0.0002). This corresponded to two clusters in the analyzed time window at each electrode site. At electrode Fz, the first cluster extended from 140 to 364 ms, and the second cluster extended from 382 to 788 ms. At electrode Cz, the effect was driven by a cluster between 136 and 356 ms, and a cluster between 372 and 902 ms. At electrode Pz, the corresponding clusters extended from 168 to 332 ms and from 360 to 806 ms. The clusters are shown in **Figure 7**. Descriptively, N2d and P3d amplitudes were time-shifted between the two conditions, giving rise to the two detected clusters. Additionally, N2d amplitudes were substantially smaller in the $Nogo_{it}$-Go condition compared to the $Nogo_{mt}$-Go condition.

Regarding group differences, the cluster-based permutation tests revealed no evidence for an effect of Group nor an interaction between Group and Condition at any of the three electrode sites. All clusters found for these effects had p-values above 0.15. The difference waves at electrodes Fz, Cz, and Pz are shown in **Figure 8** separately for the two conditions and the two groups.

DISCUSSION

In the present study, we investigated whether the postulated highly automatic pitch labeling in AP affects subsequent inhibitory processes. We used a cued auditory Go/Nogo task requiring same/different judgments for pairs of consecutively presented piano tones. In Go trials, the two piano tones were identical. In $Nogo_{it}$ trials, the second piano tone was always in-tune and differed at least one semitone from the first piano tone. In $Nogo_{mt}$ trials, the second tone was a $\frac{1}{4}$-semitone mistuned variant of the first piano tone. While the $Nogo_{it}$ condition tested if auditory-related inhibitory processes are generally altered in AP musicians, the $Nogo_{mt}$ condition tested more specifically the suppressibility of pitch labeling by

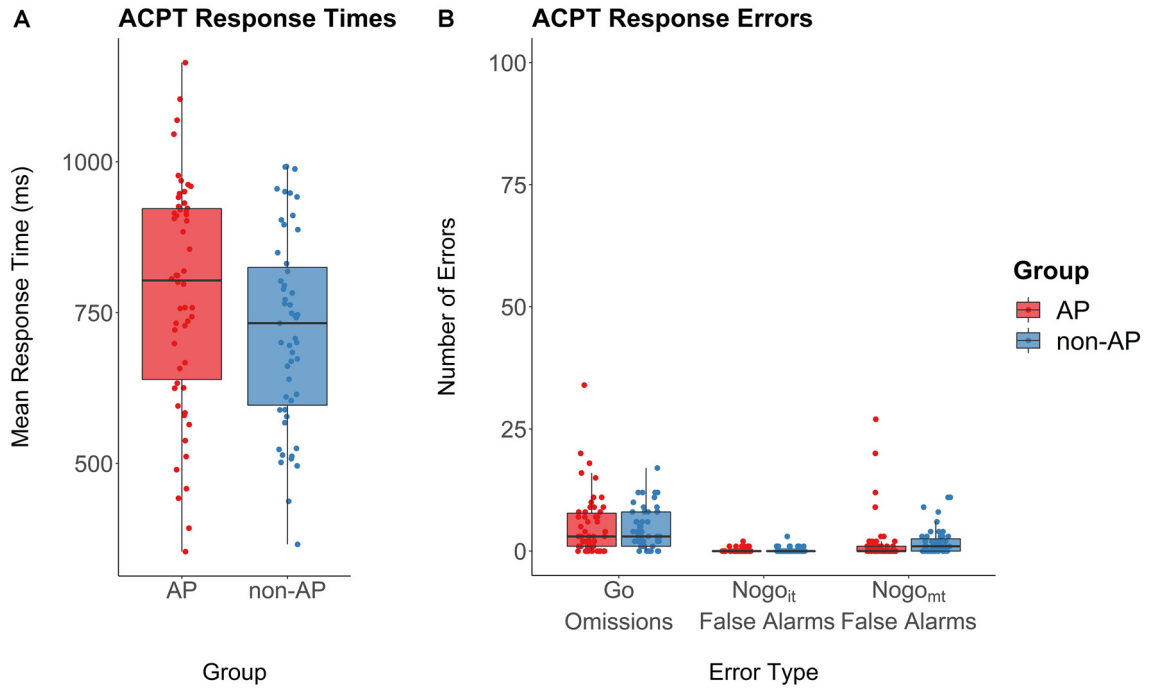

FIGURE 5 | Performance in the ACPT. **(A)** Response times in Go trials revealed no evidence for a group difference between AP musicians (red) and non-AP musicians (blue). **(B)** Response error rates for omissions (no button press in Go trials) and false alarms (failure to inhibit button press in Nogo$_{it}$ and Nogo$_{mt}$ trials). There was no evidence for a group difference with regard to the three error types.

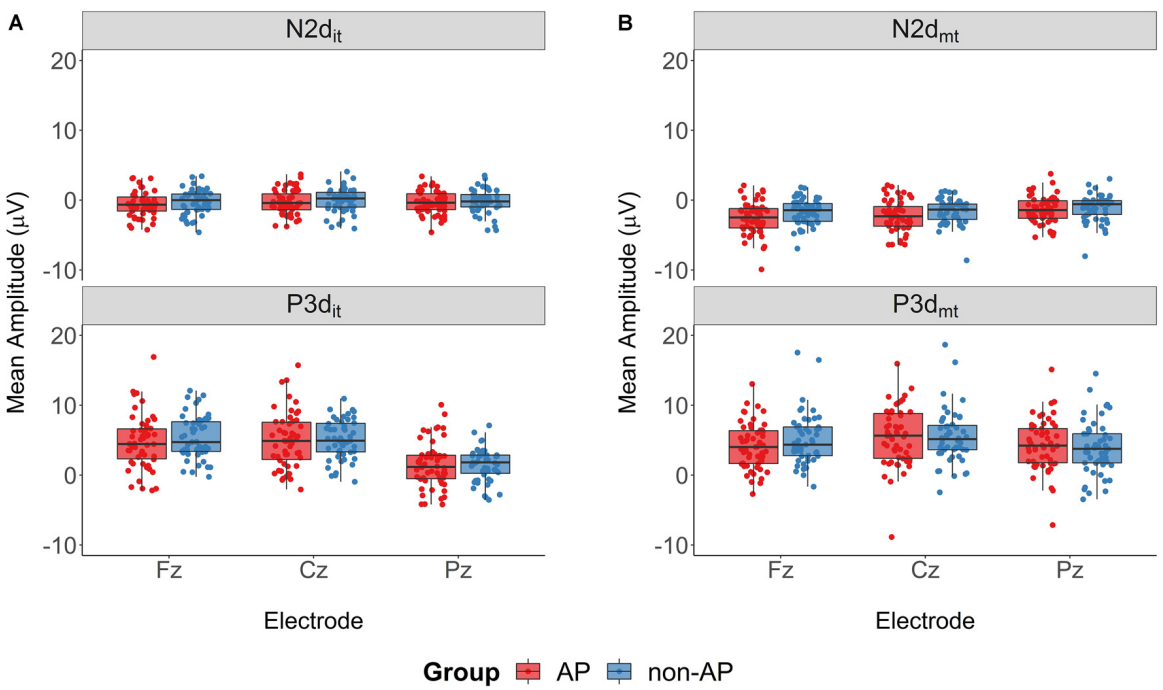

FIGURE 6 | Mean amplitudes of the ERP components. **(A)** ERP components of the Nogo$_{it}$-Go difference wave. AP musicians (depicted in red) and non-AP musicians (depicted in blue) had comparable N2d$_{it}$ and P3d$_{it}$ mean amplitudes. **(B)** ERP components of the Nogo$_{mt}$-Go difference wave. The 2 × 2 ANOVA revealed a Group × Electrode interaction for the P3d$_{mt}$ component. *Post hoc* analyses showed no evidence for a difference between AP and non-AP musicians at any electrode site.

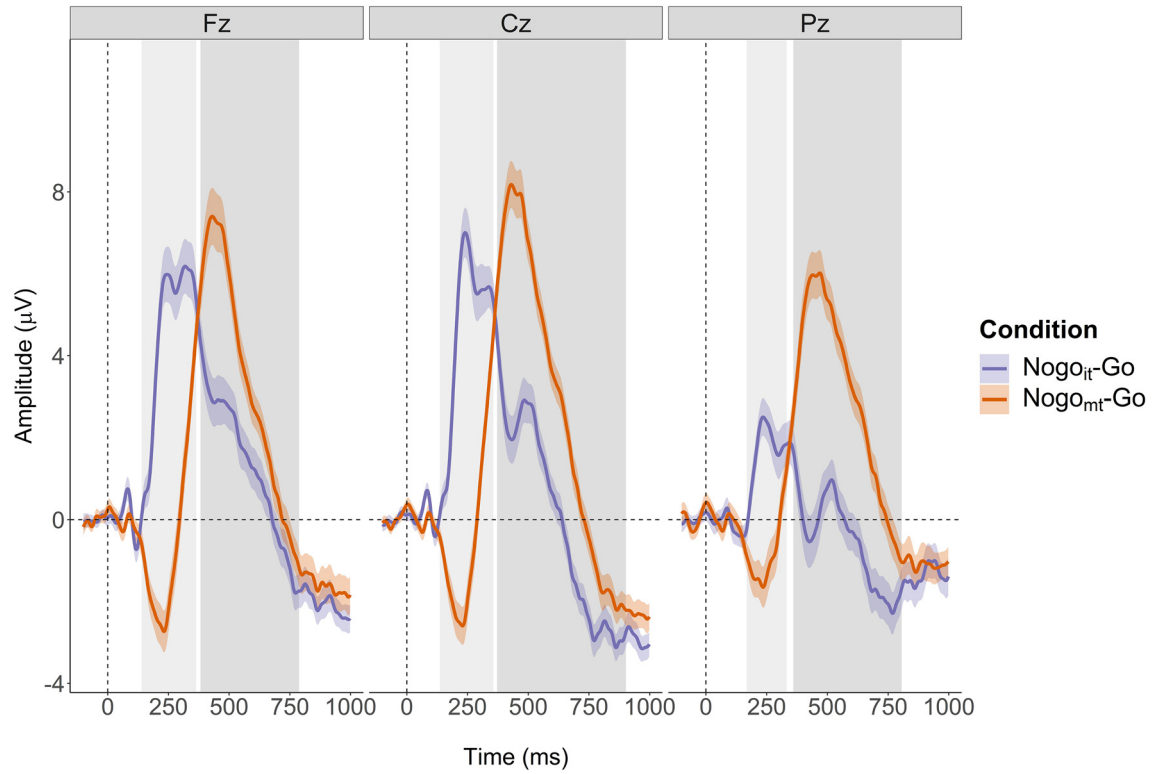

FIGURE 7 | Cluster-based permutation tests revealed a main effect of Condition at each of the three electrodes (Fz, Cz, and Pz). Clusters are indicated by grey-shaded areas. The N2d and P3d of the Nogo$_{mt}$-Go difference wave (depicted in orange) appeared later after stimulus onset than the corresponding ERP components of the Nogo$_{it}$-Go difference wave (depicted in violet). The Nogo$_{it}$-Go difference wave showed a considerably smaller N2d amplitude at all electrodes as well as a smaller P3d amplitude at electrode Pz than the Nogo$_{mt}$-Go difference wave.

introducing contradictory information about the sameness of the stimuli (same pitch class, different tone frequency). We analyzed both behavioral and electrophysiological measures to evaluate a potential change in inhibitory load in AP musicians. For the electrophysiological measures, we adopted two analysis approaches: First, we conducted a traditional ERP analysis using mean amplitudes for the N2d and P3d components. Second, we performed a cluster-based permutation analysis to test the complete ERP segment. Our data did not provide evidence for a group difference in commission errors, N2d amplitudes, P3d amplitudes, or overall difference wave ERPs for either of the two Nogo conditions. There was also no evidence for a group difference in response times and omission errors in Go trials.

Previous neurophysiological studies have repeatedly reported group differences between AP and non-AP musicians during attentive listening without labeling instruction (Zatorre et al., 1998; Ohnishi et al., 2001; Wu et al., 2008; Wengenroth et al., 2014; Burkhard et al., 2019; Leipold et al., 2019a). In the current study, we tested whether these AP-specific alterations in neurophysiological activity modify the need for inhibition. The behavioral and electrophysiological results obtained from the Nogo$_{it}$ trials do not support this hypothesis: The inhibitory processes in an auditory Go/Nogo task do not seem to have been influenced by absolute pitch. Whether or not the differential tone processing affects subsequent cognitive processes and the associated neurophysiological measures, may strongly depend on the specific task. Such a dependence of AP-specific effects on situational factors has previously been demonstrated with regard to the influential finding of reduced P3b amplitudes in AP musicians in active auditory oddball tasks (Klein et al., 1984). Since the P3b is thought to reflect working memory processes (for a review, see Kok, 2001; Polich, 2007), it was inferred from the original finding of smaller P3b amplitudes that AP musicians may not need to update their working memory during the task because they can access permanent pitch templates. Some of the subsequent studies replicated the effect (Hantz et al., 1992; Wayman et al., 1992; Crummer et al., 1994) while others did not (Hantz et al., 1995; Hirose et al., 2002). Bischoff Renninger et al. (2003) integrated these heterogeneous findings by demonstrating that the AP musicians employed different listening strategies (i.e., absolute pitch or relative pitch) depending on task difficulty and task instruction. Active oddball tasks are structured similarly to Go/Nogo tasks, but target tones appear only infrequently (Kropotov, 2009). The instruction to focus on tone-frequency changes in the current study might have encouraged a relative-pitch rather than an absolute-pitch listening strategy, preventing us from observing AP-specific effects.

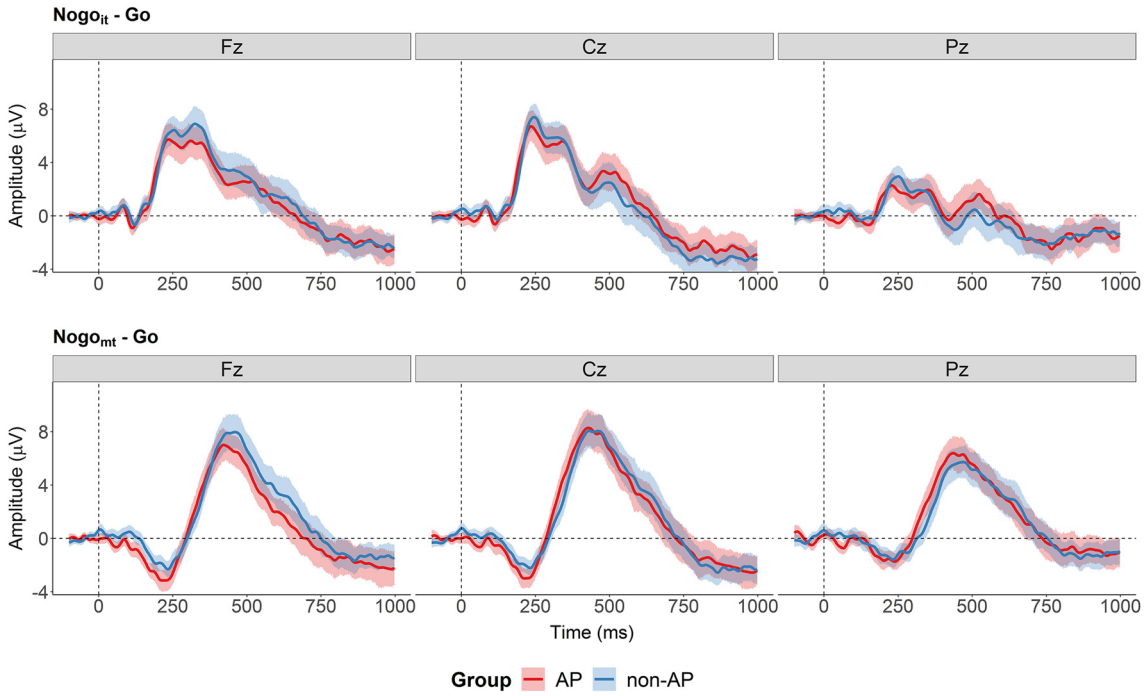

FIGURE 8 | Difference waves separately for the two groups at the three electrodes (Fz, Cz, and Pz). Cluster-based permutations tests provided no evidence for a group difference between AP and non-AP musicians at any of the electrodes of the difference waves. The shaded areas represent the 95% between-subject confidence interval.

Furthermore, the listening instruction might not only influence later task-related cognitive processes in AP musicians but also the differential tone processing *per se*. As described above, group differences between AP and non-AP musicians in neurophysiological activity have been repeatedly observed during attentive listening. However, in several studies, the mismatch negativity, an ERP component evoked during passive listening in passive oddball tasks, did not differ between AP and non-AP musicians (Tervaniemi et al., 1993; Rogenmoser et al., 2015; Greber et al., 2018). Thus, the focus of attention could play a role in whether and to what extent subprocesses of pitch labeling and associated neurophysiological activations are automatically triggered by acoustic stimuli. In the current study, participants did have to pay close attention to the presented tones but were instructed to concentrate on one specific dimension of the stimuli (i.e., the sameness of tone frequency), which was independent of the pitch class. In contrast to findings during attentive listening without an additional task (Burkhard et al., 2019), the visual inspection of the group-averaged ERPs (**Figure 2B**) shows comparable N1 and P2 amplitudes in response to the Go stimulus for AP and non-AP musicians. This could indicate that the AP-specific neurophysiological activity thought to be automatically induced by simply listening to tones was not present in our task, and, consequently, no additional inhibitory efforts would have been required.

Finally, it is also possible that the measures used in the current study were simply not sensitive enough to capture subtle group differences in inhibition. For instance, a ceiling effect occurred for both AP and non-AP musicians' task performance, which was most evident in Nogo$_{it}$ trials. Since the musicians had no difficulty solving the task, possibly the small increases in inhibitory loads did not show up in the error rates.

Compared to the Nogo$_{it}$ condition, the Nogo$_{mt}$ condition additionally evaluated whether the AP musicians were able to suppress conflicting pitch-labeling information. The assumption that pitch-labeling information is difficult to suppress stems mainly from auditory Stroop tasks (Miyazaki, 2004; Itoh et al., 2005; Hsieh and Saberi, 2008; Akiva-Kabiri and Henik, 2012; Schulze et al., 2013). Usually, AP musicians are asked to name a sung syllable or to label a visually presented note while ignoring the pitch of the sung syllable or a simultaneously presented musical tone. AP musicians reliably show an increased interference effect of incongruent stimuli or incongruent stimulus dimensions compared to non-AP musicians. Consistent with the literature, our behavioral auditory-visual Stroop task evoked a greater incongruence effect in AP musicians than in non-AP musicians. This suggests that the auditory-visual Stroop task did activate pitch-labeling processes in our sample of AP musicians, which then interfered with the labeling of the visual notes.

In Nogo$_{mt}$ trials, tone frequency and pitch class of the second stimulus also provided contradictory information in a Stroop-like manner. Hence, we expected that—analogous to the Stroop task—AP musicians would process both the task-relevant (i.e., tone frequency) and the task-irrelevant

stimulus dimension (i.e., pitch-class) due to the automaticity of pitch labeling, resulting in an increased inhibitory load compared to non-AP musicians. Instead, we found no evidence for a group difference in behavioral or electrophysiological measures for $Nogo_{mt}$. These results suggest that AP musicians can successfully control irrelevant pitch-label information in the context of a Go/Nogo task with same/different judgments. Given the results from the Stroop task, it appears that the task context and the corresponding task demands might critically influence whether conflicting pitch-labeling information hinders performance. Contrary to incongruent trials in the Stroop task, the pitch label (e.g., "C") of the second tone—considered in isolation—had no semantic overlap with the required response (i.e., "different") in the $Nogo_{mt}$ trials. Rather the information extracted from the pitch labels of both tones (e.g., C followed by C equals the same pitch label; "same") did not match the information of the tone frequency comparison (i.e., different tone frequencies; "different"). Contradictory pitch-labeling information might predominantly impair performance when the task itself specifically requires a response of the same semantic category (i.e., a musical label as in naming a visual note or a sung tone label). A recent study investigated the strength of association between pitch information and verbal labels in musicians using a Stroop paradigm (Sharma et al., 2019). The study included three different Stroop tasks that required high pitch/low pitch judgments of sung syllables tuned to either 261.3 Hz (C4; low) or 392 Hz (G4; high). The sung syllables could be congruent or incongruent with the pitch height in terms of English words (/low/ and /high/), English solemnizations (/do/ and /so/), or key notations (/see/ and /jee/). The incongruence effect on response times was attenuated for solemnizations compared to English words in both AP and non-AP musicians. For key notations, there was no evidence for an incongruence effect on response times. It appears that the verbal labels were semantically not as strongly mapped to the high/low response. Most interestingly, this was even the case for AP musicians. Although the sung label (as keycode or solemnization) was semantically incongruent with the pitch-labeling information, they showed comparable incongruence effects on response times as non-AP musicians. Linguistic information conflicting with pitch-labeling information did not further impair the task performance of AP musicians for high/low judgments. It should be noted that the AP musicians but not the non-AP musicians did show a significant incongruence effect on ERP measures in the keycode task. However, the absence of evidence for an incongruence effect in non-AP musicians is not sufficient to conclude that there is a group difference without a direct statistical group comparison of the effect. Taken together, AP musicians may be able to ignore task-irrelevant conflicts with pitch-labeling information depending on the specific task and context. Considering that automatic processes are often described as obligatory, stimulus-driven, and requiring little to no attention (Palmeri et al., 2004; Palmeri, 2006), the findings of the current study may indicate that pitch labeling in AP is less automatic than previously assumed.

It is, however, important to note that the evidence in favor of H0 as indicated by the Bayes factors was only anecdotal or inconclusive ($BF_{01} < 3$). To get more conclusive evidence within the Bayesian framework (i.e., that there is no difference between the ERPs of the two groups, or that there is a group difference), an even larger sample would be needed. Unfortunately, due to the rarity of AP as well as the time-consuming and resource-intensive data acquisition in neuroscience, it is challenging for a single research group to recruit large numbers of AP musicians. For future research, collaborations between multiple research groups might be helpful in this regard.

While there was no evidence for a group difference, the cluster-based permutation analysis did reveal an effect of condition for the ERP difference waves. Visual inspection of the two corresponding clusters (compare **Figure 7**) shows that the N2d of the $Nogo_{it}$-Go ERP was vanishingly small at all electrodes analyzed (Fz, Cz, and Pz) whereas the N2d of the $Nogo_{mt}$-Go ERP was more pronounced and prolonged. Also, the P3d was latency-shifted and slightly larger for the $Nogo_{mt}$-Go ERP compared to the $Nogo_{it}$-Go ERP.

Small or even absent N2 effects as in $Nogo_{it}$ have been repeatedly observed in auditory Go/Nogo tasks (Schröger, 1993; Falkenstein et al., 1995, 1999, 2002; Kiefer et al., 1998). Initially, this phenomenon was attributed to the stimulus modality, as visual stimuli seemed to consistently elicit larger N2 effects (e.g., Falkenstein et al., 1995, 1999, 2002). However, later studies could demonstrate that the relative N2 amplitude may depend more on the perceptual overlap between target and non-target stimuli than on the modality (Nieuwenhuis et al., 2004; Azizian et al., 2006; Smith and Douglas, 2011). Non-target stimuli that are more similar to the target stimulus may generate a stronger tendency to (erroneously) respond, and, thus, require greater inhibition efforts (Azizian et al., 2006). Differences in perceptual similarity could explain the N2d condition difference found in the present study. In $Nogo_{mt}$ trials, the target and the non-target stimuli were much more similar ($\frac{1}{4}$-semitone difference) than in $Nogo_{it}$ trials (difference of at least one semitone). This was paralleled by an increase in N2d amplitude. The more pronounced and prolonged N2d for $Nogo_{mt}$ then probably shifted the latency of the P3d. The P3d itself likewise showed a larger amplitude for $Nogo_{mt}$ than for $Nogo_{it}$, mainly noticeable at the parietal electrode Pz. Hence, the amplitude of the P3d might have also been sensitive to the degree of perceptual overlap. An increase in both amplitude and latency of Nogo-P3 due to higher stimulus similarity has been previously reported for visual stimuli (Azizian et al., 2006). A second study, on the other hand, found comparable P3 effects for similar and dissimilar stimuli in the auditory and visual domain (Smith and Douglas, 2011). However, even the similar acoustic stimuli there differed by 165 cents (1,000 Hz/1,100 Hz; a difference of about one and a half semitone) compared to 25 cents in the current study. Thus, the P3 effect might only be affected by a very high perceptual overlap.

Even though the condition effect appears to be consistent with previous findings on the perceptual similarity between target and

non-target stimuli, we cannot exclude the possibility that the ERPs were additionally modulated by the tuning or mistuning of the tones. In our Go/Nogo task, the first piano tone was always in-tune in Go, $Nogo_{it}$, and $Nogo_{mt}$ trials because the intonation context can influence the pitch classification in AP musicians (Van Hedger et al., 2018). By constantly providing in-tune tones, we hoped to ensure that the AP musicians' internal intonation matched the intonation of the tones. This, combined with the frequency spacing applied, resulted in the second tones being mistuned in all $Nogo_{mt}$ trials and being in-tune in all $Nogo_{it}$ trials. Therefore, we are not able to distinguish the contributions of the tuning of the second stimulus (in-tune vs. mistuned) from the contributions of the frequency distance between the first and second stimulus ($\geq$1 semitone in $Nogo_{it}$ vs. $\frac{1}{4}$ semitone in $Nogo_{mt}$) to the condition difference. To disentangle these two effects, future studies could use mistuned tones with a greater frequency distance to the first stimulus (e.g., D4 followed by a sharp-mistuned F4). This would also allow to include non-musicians in the sample to evaluate the influence of musical experience, which unfortunately was not feasible with the current task paradigm. During pilot-testing, participants without musical training were not able to discriminate the $\frac{1}{4}$-semitone frequency changes in $Nogo_{mt}$ trials. The small number of correct trials resulted in too few EEG segments (i.e., between one and six out of 100 $Nogo_{mt}$ trials) to compute reliable ERPs. It is well established that non-musicians have higher discrimination thresholds than musicians (Spiegel and Watson, 1984; Micheyl et al., 2006). We, nevertheless, have deliberately chosen the $\frac{1}{4}$-semitone difference so that the second tone would still be recognized by AP musicians as belonging to the same pitch category as the first tone. Had we chosen a larger frequency difference (e.g., $\frac{1}{2}$ semitone) to the first tone (e.g., E4), the second tone might have been assigned to a different pitch category (e.g., E4♯ or E4♭).

Further limitations of our study concern the pitch-labeling task. As can be seen in **Figure 4A**, the pitch-labeling scores overlapped between the two groups, with some self-identified AP musicians performing worse than some self-identified non-AP musicians. This overlap may be attributed to three features of our pitch-labeling task. First, because participants had to choose one out of 36 possible response options, each trial could last up to 15 s. This relatively long response window was shown to be necessary during pilot tests. Unfortunately, this may have allowed some of the non-AP musicians to use their relative-pitch ability to solve the task. One possibility to better distinguish AP and non-AP musicians based on pitch-labeling performance would be to include both response accuracy and latency information in a combined score (as suggested by Bermudez and Zatorre, 2009). The reconstruction of pitch labels based on a relative-pitch strategy is expected to take more time than genuine AP (see also Miyazaki, 1990). In the current study, the online implementation in an unstandardized setting at home (e.g., some participants used a computer mouse, some a touch screen, and others the trackpad of their laptop to submit the responses) in combination with the 36-item multiple-choice format did not allow to collect meaningful response time data. Future studies could reduce the item list by only asking for the pitch chroma irrespective of the octave. For accurate response time measures, the response options could then be arranged in a circular shape with equal distance to the starting point of the cursor (e.g., as done in Sharma et al., 2019). Another possibility for a better distinction between AP and non-AP musicians would be to prevent non-AP musicians from accessing relative-pitch cues. Wengenroth et al. (2014) proposed inserting non-harmonic and distorted interference stimuli between the tones for this purpose. For AP musicians, unpublished data from our lab (n = 39) suggests a strong correlation (r = 0.7) between our online pitch-labeling task and the original paper-pencil test of our group (Oechslin et al., 2010), which had shorter interstimulus intervals (4 s) and was conducted in a controlled setting. Thus, the longer interstimulus interval in the online implementation probably affects non-AP musicians more strongly than AP-musicians.

A second feature of the pitch-labeling task that might have affected the score distribution is the use of pure tone stimuli. Pure tones do not give an advantage to any specific group of instrumentalists based on their familiarity with a timbre (see Takeuchi and Hulse, 1993). However, pitch identification is generally more challenging for pure tones than for instrumental sounds (Miyazaki, 1989; Gruhn et al., 2019). In a study by Van Hedger and Nusbaum (2018), self-reported AP possessors achieved an accuracy between 75% and 100% (mean: 95.4%) for a mixture of piano and guitar tones, but only an accuracy between 25% and 100% (mean: 56.4%) for pure tones. In our sample of AP musicians, the accuracy for pure tones was even slightly higher (range: 36.1%–100%, mean: 76.4%). Therefore, it is very well possible that our AP musicians would similarly have shown higher accuracy rates for instrumental sounds. Future studies might want to consider including both pure and instrumental tones to get a better estimate of pitch-labeling ability.

Third, the tones in the pitch-labeling test were tuned to a standard reference of A4 = 440 Hz. This might have disadvantaged AP musicians who often play music tuned to a different reference tone (e.g., baroque tuning). Studies that categorize AP and non-AP musicians based on pitch-labeling performance could incorporate information about the musicians' primary reference tone in the scoring procedure.

Within our AP project, the pitch-labeling task was designed as an additional validation tool only. As set out above, it is not optimally suited to distinguish AP musicians from non-AP musicians by itself. Most importantly, using self-report, we did not have to apply an arbitrary cutoff for group construction and did not risk erroneously assigning well-performing non-AP musicians to the AP group.

CONCLUSION

The current study provided no evidence for an effect of AP on behavioral or neurophysiological measures of inhibition in a cued auditory Go/Nogo task. The results from the $Nogo_{mt}$ condition further suggest that AP musicians can suppress pitch-labeling information depending on the task demands. Given the results from the bimodal Stroop task, it remains unclear under which circumstances subprocesses of pitch labeling are activated

and to what extent these processes can be considered automatic. While the ERPs were not modulated by AP, there was a condition difference between the two Nogo conditions which probably reflects a modulation by the perceptual similarity between target and non-target stimuli.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Open Science Framework: https://osf.io/f5nkx/.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Kantonale Ethikkommission Zürich. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MG and LJ designed research and wrote the article. MG performed research and analyzed data. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2020.585505/full#supplementary-material.

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Chapter 5 General Discussion

This thesis explored and re-examined the neural bases of AP. We analyzed EEG data of a large sample of musicians with and without AP. The data were acquired during one task-free condition and two pitch-processing tasks that did not require explicit pitch labeling. Two of the studies included replication attempts of previous findings. Overall, we found little evidence for strong differences in EEG activity between AP musicians and non-AP musicians in the studied conditions.

In article 1 (Greber et al., 2018), we repeated a previous experiment of our research group (Rogenmoser et al., 2015) in a sample four times as large as in the original study. Consistent with the original study as well as earlier work (Tervaniemi et al., 1993), we found no evidence for an effect of AP on the MMN during passive tone listening. We were also able to replicate condition-specific effects on both the MMN and the P3a across all participants. However, contrary to the original study, there was no evidence that the P3a amplitudes were smaller in AP musicians than in non-AP musicians. Taken together, our data did not provide evidence in favor of group differences in ERP measures during passive tone listening, neither in pre-attentive (i.e., MMN) nor in early cognitive processing (i.e., P3a).

Article 2 (Greber et al., 2020) focused on intrinsic functional connectivity to determine the contributions of sensory and higher-order brain regions to AP. Replicating the region-of-interest approach of a previous study (Elmer et al., 2015), we were not able to confirm the AP-specific increase in theta connectivity between the left auditory cortex and the left DLPFC in our larger sample. In the additional exploratory whole-brain analyses, we detected three networks with increased connectivity in the theta and lower-beta frequency band in AP musicians compared to non-AP musicians. The brain regions involved in these networks corroborate the importance of both sensory and higher-order regions in the perisylvian area for AP, but differences between AP and non-AP musicians were overall very subtle.

The final article (Greber & Jäncke, 2020) describes an auditory Go/Nogo task requiring same/different decisions. The task included two different Nogo conditions to test whether auditory inhibition processes generally differ between AP and non-AP musicians and whether incongruent pitch-labeling information can be suppressed. For both Nogo conditions, we found no evidence for a group difference in behavioral measures and ERPs. Our results indicate that AP musicians were able to suppress irrelevant pitch-labeling information and raise the question to what extent subprocesses of AP are automatically activated upon hearing a periodic sound.

5.1 Automaticity of AP

One of the presumed key features of AP is the automaticity of pitch labeling (Levitin & Rogers, 2005). A cognitive process is usually considered automatic (as opposed to controlled) if it is fast, effortless, stimulus-driven, obligatory, and/or requires little to no attention (Palmeri, 2006; Palmeri et al., 2004). When asked to identify pitches, AP musicians do so accurately, effortlessly, and quickly (e.g., Bermudez & Zatorre, 2009; Miyazaki, 1990; Wilson et al., 2009). In addition, AP musicians show interference effects of pitch labeling in auditory Stroop tasks (Akiva-Kabiri & Henik, 2012; Hsieh & Saberi, 2008; Itoh et al., 2005; Miyazaki, 2004b; Schulze et al., 2013), indicating that pitch labeling is difficult for them to suppress. In the third study of this thesis, we included our own auditory variant of the Stroop task (first published in Leipold, Greber, Sele, et al., 2019) and were able to confirm the typical incongruence effect in our sample. Apart from behavioral characteristics suggesting automaticity of pitch labeling, AP musicians have also been reported to show increased neurophysiological activity in response to periodic sounds in several brain regions even when they were not asked to identify the corresponding pitch (Burkhard et al., 2019; Leipold, Brauchli, Greber, & Jäncke, 2019; Ohnishi et al., 2001; Wengenroth et al., 2014; Zatorre et al., 1998). These findings suggest that at least some subprocesses of AP (if not necessarily pitch labeling) are automatically activated.

The passive auditory oddball task in the first article of this thesis and the auditory Go/Nogo task in the third article allowed us to study the automaticity of AP under

conditions that did not require explicit pitch labeling. In the passive auditory oddball task, participants focused on a silent black and white film while a series of piano tones was simultaneously presented. The participants were instructed to ignore the tones. Group differences in the ERP measures would have indicated that pitch processing in AP is altered even when the tones are not attended. In the Go/Nogo task, participants had to judge whether two successive piano tones were identical or not. The pitch class of the tones was irrelevant to the task but was incongruent in a Stroop-like manner with the required response in the second of two Nogo conditions. Group differences in the analyzed ERPs would have indicated that pitch processing was generally altered in AP (ERP in the Go condition; no inhibitory processes involved), that the inhibitory processes in the Nogo condition were affected by this alteration (ERP in the first Nogo condition), and/or that conflicting pitch-labeling information cannot be suppressed (ERP in the second Nogo condition). In both experiments, the data provided no evidence for group differences between AP and non-AP musicians in the ERP measures. Thus, AP processing might not be as stimulus-driven and automatic as is often assumed. Whether and to what extent periodic sounds trigger AP processes in AP possessors may rather strongly depend on the specific task.

A task dependence of AP processing is also implied by the literature on early auditory ERP components. During attentive listening, AP musicians have been reported to show an increase in the N1 component compared to non-AP musicians (Burkhard et al., 2019) or even an additional early component called the AP negativity (Itoh et al., 2005; but see Leipold, Oderbolz, Greber, & Jäncke, 2019). By contrast, several studies investigating the N1 and its magnetic equivalent during passive listening found no evidence for differences between AP and non-AP musicians (ignoring tones without distraction task: Hirose et al., 2005; Wu et al., 2008; ignoring tones while watching cartoon videos: Pantev et al., 1998). Wu et al. (2008) observed that the estimated source activity of the N1 differed between AP and non-AP musicians during a labeling condition but not during passive listening or during a relative-pitch task. The participants' focus of attention appears to play an important role in whether differences in early stages of pitch processing can be observed between musicians with and without AP.

Later stages of pitch processing in AP possessors have likewise been proposed to be affected by task demands. Bischoff Renninger et al. (2003) showed that whether or not the P3b component is reduced in AP possessors during an active auditory oddball task (Klein et al., 1984) depends on the chosen listening strategy (i.e., RP or AP). This is in turn likely to be influenced by the task difficulty and the task instruction (Bischoff Renninger et al., 2003). The authors also found that AP possessors were able to ignore pitch-specific information when asked to focus on relative-pitch aspects of the stimuli (i.e., higher/lower judgments). It is possible that our Go/Nogo task with same/different judgments (article 3) encouraged the AP musicians to use an RP listening strategy, preventing us altogether from measuring AP processing. The task context might also explain the seeming discrepancy between the results from the behavioral Stroop task and the results from the Stroop-like condition in the Go/Nogo task. Unlike the same/different task, the note naming in the behavioral Stroop task probably did activate pitch-labeling processes.

To further elucidate the automaticity of AP processes, future studies could more systematically examine the neurophysiological activity of AP and non-AP musicians during different listening conditions. These could range from passive listening to explicit pitch-naming tasks (e.g., ignoring the tones with a distractor task; ignoring the tones without a distractor task; attentively listening to the tones; focusing on different aspects of the tones, such as loudness or timbre or pitch; relative-pitch judgments; explicit pitch identifications). To improve our understanding of the strength of pitch-label associations and of the conditions that trigger unintentional pitch labeling in AP possessors, different variants of auditory Stroop tasks (e.g., as in Sharma et al., 2019) could be tested.

5.2 Perception and Cognition in AP

The first and the second study of this thesis addressed the role of early and late auditory processes in AP. The knowledge about the perceptual and/or cognitive functions enabling AP is still limited. Based on evidence from behavioral and neuroscientific studies, different cognitive models have been developed. Some suggest an early perceptual

component (e.g., Kim & Knösche, 2017a; Ross et al., 2005; Zatorre, 2003), while others focus on later higher-level processes (Levitin, 1994; Levitin & Rogers, 2005).

Emphasizing the importance of early processing stages, a considerable number of neuroscientific studies has revealed AP-specific alterations in the structure and function of the auditory cortex. In a seminal paper, Schlaug et al. (1995) found that the typical leftward asymmetry of the planum temporale was stronger in musicians with AP than in musicians without AP. This finding was later replicated and mostly attributed to a smaller right rather than a larger left planum temporale in AP musicians (Keenan et al., 2001; Luders et al., 2004; Wilson et al., 2009; but see Zatorre et al., 1998). Cortical thickness of the superior temporal gyrus was also shown to be left-lateralized but bilaterally increased (Dohn et al., 2015), and the volume of Heschl's gyrus was found to be larger in AP musicians (bilaterally: McKetton et al., 2019; in the right hemisphere: Wengenroth et al., 2014). As recently reported, the enlargement of the Heschl's gyrus might subserve broader frequency tuning in the primary auditory cortex and the rostral part of the auditory cortex (McKetton et al., 2019). The planum polare, which lies anterior to the Heschl's gyrus, has been found to be more richly myelinated in AP musicians (Kim & Knösche, 2016) and functionally more strongly connected to anteroventral areas of the auditory cortex during fMRI resting state than in non-AP musicians (Kim & Knösche, 2017b). Further functional studies found greater EEG source activity in the right Heschl's gyrus during tone listening (Burkhard et al., 2019), greater EEG source activity in bilateral auditory regions during tone labeling (Wu et al., 2008), increased fMRI and MEG activity in the right planum temporale during tone listening (Leipold, Brauchli, Greber, & Jäncke, 2019; Wengenroth et al., 2014), differential local connectivity patterns in the left auditory cortex during resting state (Brauchli et al., 2019), and a positive relationship between AP proficiency and activity in the left planum temporale during music listening (Ohnishi et al., 2001). Adjacent to the auditory cortex, an increase of fMRI activity was also observed in the left superior temporal sulcus during the early perceptual phase of a pitch memory task (Schulze et al., 2009). Findings like these are often considered indicative of differential perceptual and/or early encoding processes in AP, such as refined pitch categorization (Zatorre, 2003).

On the other hand, differences between AP and non-AP possessors have also been observed in higher-order brain regions. Various studies have reported structural and functional differences between AP and non-AP possessors in the inferior frontal gyrus (Dohn et al., 2015; Leipold, Brauchli, Greber, & Jäncke, 2019; McKetton & Schneider, 2018; Schulze et al., 2009; Wengenroth et al., 2014; Zatorre et al., 1998). These have been related to a verbal component (Wengenroth et al., 2014) or a reduced working-memory load in AP (Leipold, Brauchli, Greber, & Jäncke, 2019). Activity in the DLPFC has also been linked to AP, specifically to the retrieval of pitch-label associations (Bermudez & Zatorre, 2005; Ohnishi et al., 2001; Zatorre et al., 1998; but see Leipold, Brauchli, et al., 2019). In addition, results from several EEG studies suggest that AP musicians differ from non-AP musicians in late rather than early stages of pitch processing (Elmer et al., 2013; Leipold, Greber, et al., 2019; see also Crummer et al., 1994; Hantz et al., 1992; Klein et al., 1984; Wayman et al., 1992). The two studies we attempted to replicate had provided further evidence for the importance of late processing stages. Rogenmoser et al. (2015) found group differences in the P3a ERP component but not in the preceding MMN during passive listening. Elmer et al. (2015) found that the intrinsic theta connectivity between the left auditory cortex and the left DLPFC was stronger in AP musicians than in non-AP musicians; a finding that suggests that auditory and frontal regions may act in concert to make AP processing possible.

For a deeper understanding of the neural bases of AP, attempts to integrate the reported alterations in sensory and higher-order brain regions are vital (see Leipold, Greber, & Elmer, 2019). While our replications could not confirm Rogenmoser et al.'s (2015) and Elmer et al.'s (2015) findings, the exploratory whole-brain analysis of intrinsic connectivity in article 2 did provide some evidence that sensory and higher-order brain regions around the sylvian fissure (e.g., planum temporale, inferior frontal gyrus, parietal operculum, and middle temporal gyrus) may work together in AP processing. However, despite the large sample by the field's standards, the effects were very subtle, and the findings clearly warrant replication. Given that AP processing might not be as automatically activated as previously assumed (compare Chapter 5.1 Automaticity of AP), it is conceivable that the brain networks underlying AP are generally difficult to measure during rest. As of yet, resting-state studies have yielded heterogenous results on the effect of AP, ranging from global hyperconnectivity (Loui et al., 2012) to regional

hyperconnectivity (Brauchli et al., 2019; Kim & Knösche, 2017b) to global hypoconnectivity (Wenhart et al., 2019) to even no measurable differences between AP and non-AP musicians (Brauchli et al., 2020; Leipold et al., 2021). This inconsistency, too, may be an indication that the true effects of AP on intrinsic connectivity — if any at all — are small. Investigating functional connectivity during acoustic stimulation (e.g., during music listening: Brauchli et al., 2020) seems necessary to get a clearer picture of which and how sensory and higher-order brain regions jointly contribute to a potential AP network.

The heterogenous activity patterns in the brain even during active conditions call for an explanation beyond connectivity analyses. Up until now, it is unclear if the heterogeneity can be attributed to the large variety of applied methods (i.e., neuroimaging technique, specific task and stimuli, data preprocessing, type of statistical analysis) or if it is related to low statistical power due to small sample sizes. Direct replications and studies with larger sample sizes can help shed light on the influencing factors.

5.3 Significance of Replication Studies in AP Research

Article 1 and article 2 of this thesis reported replication attempts of previously found AP effects on neural activity. Replications are a crucial part of the scientific method. They help assess the robustness of findings and improve the estimation of effect sizes. This seems particularly relevant in research fields where samples sizes are bounded by inherent limitations, such as the rarity of a specific population group or resource-intensive data acquisition — as is both the case in neuroscientific AP research.

Under the radar, replications (in a broader sense) have already substantially contributed to our understanding of AP. Early anecdotal observations, such as a shift in pitch perception with increasing age (Profita & Bidder, 1988; Vernon, 1977; Wynn, 1992), have later been empirically confirmed in large-scale studies (e.g., Athos et al., 2007). The finding of Levitin (1994) that most people without AP can reproduce popular songs at or near the original pitch was replicated by later studies (Frieler et al., 2013; Jakubowski & Müllensiefen, 2013), corroborating his claim of a widespread latent pitch memory. In

neuroscience, the larger asymmetry of the planum temporale in AP reported in an early structural study (Schlaug et al., 1995) could be solidified by subsequent studies (Keenan et al., 2001; Luders et al., 2004; Wilson et al., 2009). But replications do not only increase — or, in case of replication failure, decrease — confidence in scientific claims, they also have the potential to generate new knowledge and hypotheses. This was, for instance, the case with the first finding of ERP differences between AP musicians and non-AP musicians (Klein et al., 1984). The reported reduction of P3b amplitudes in AP processing was successfully replicated by several studies (Crummer et al., 1994; Hantz et al., 1992; Wayman et al., 1992), but other studies failed to observe the effect (Hantz et al., 1995; Hirose et al., 2002; Johnston, 1994, as cited in Bischoff Renninger et al., 2003). Based on these contradictory results, Bischoff Renninger et al. (2003) set out to determine potential factors influencing the effect. They could show that subtle differences in the task as well as individual differences in RP and AP skills can affect the listening strategy AP possessors choose. Most findings in the neuroscientific AP literature, however, have yet to be replicated.

Our own replications have provided valuable insights both on the level of the research questions and on the level of AP research in general. The successfully replicated null results in article 1 (i.e., no group differences for the MMN) added to the evidence that AP musicians do not excel in detecting changes in tone frequency (Fujisaki & Kashino, 2002; Rogenmoser et al., 2015; Sergeant, 1969; Tervaniemi et al., 1993). The non-replications further indicate that the previously reported AP effects (Elmer et al., 2015; Rogenmoser et al., 2015) should be interpreted with caution. Additional studies are needed to draw a definite conclusion if and under what circumstances these effects are present. More generally, the unsuccessful replication attempts of this thesis and of a third study within the same research project (Leipold, Oderbolz, Greber, & Jäncke, 2019) highlight the need for well-powered replication studies in neuroscientific AP research. In a research field with only a small number of studies, each study has an impact on the overall picture. Only by assessing the robustness of the findings can we advance the knowledge about the neural mechanisms underlying AP. I hope that the willingness to invest resources into replicatory work demonstrated by our research project inspires further replications in the field.

5.4 Future Directions

As a relatively new research area, cognitive neuroscience has only just begun to uncover the neural bases of AP but promises a deeper understanding of the phenomenon and thereby of auditory processing and auditory memory in general. The articles of this thesis have called into question the automaticity of AP, emphasized the importance of the task context for AP processing, and raised awareness of reproducibility issues. To live up to its promise, future research needs to address the factors that potentially contribute to the current discrepancy in neuroscientific AP literature: the small sample sizes, the lack of standardized operationalization of AP, and the multitude of different methods.

5.4.1 Standardization of AP Classification

One of the main issues in AP research is the lack of a standard for assessing the ability. The problem has long been recognized (see e.g., Oakes, 1955; Takeuchi & Hulse, 1993), but despite a general awareness in the community, no consensus has yet been reached. In 2009, Bermudez and Zatorre (2009) developed and validated a computerized pitch-identification test in the hopes of standardizing the behavioral assessment of AP and collecting data across multiple research centers. To my knowledge, the endeavor has unfortunately not succeeded: Most research groups still use their own AP tests. With the advent of data sharing through open data repositories, the distribution might now be easier to achieve. However, the challenge remains to unify the many different views on how to optimally test pitch naming (e.g., whether to include noise between the stimuli to prevent the use of RP strategies, what type of stimuli to use, whether to set a time limit for responses, how to take into account that not all participants are accustomed to the same tuning standard). Perhaps a standardized AP test would become more widely accepted if it were not designed by a single research group but rather by a task force of AP scientists with different backgrounds (e.g., musicologists, cognitive psychologists, neuroscientists, geneticists).

Pitch-identification tasks may generally not be best suited to determine if a person has AP. They rely on a finite number of response options, allowing for a much higher chance level of getting the correct answer than, for example, pitch-production tasks (Takeuchi &

Hulse, 1993). For this reason, Takeuchi and Hulse (1993) recommended that a standardized measure of AP should account for the performance in both pitch identification and pitch production. In the long run, this might at the very least help clarify the relationship between active and passive AP (see Dohn et al., 2014). It might also be worth considering including a task that does not require knowledge of note names (e.g., Ross et al., 2004) to verify the strictly musical definition of AP.

A common limitation of all behavioral tests remains that a threshold needs to be defined to distinguish AP possessors from non-AP possessors. To avoid arbitrary cut-offs, we based the group assignment in our studies on self-report and used pitch-identification performance to validate it. Self-report of AP tends to be fairly consistent with the performance in AP tests (e.g., Athos et al., 2007; Baharloo et al., 1998; Bermudez & Zatorre, 2009; Gregersen et al., 2013), and it avoids accidental assignment of well-performing non-AP possessors to the AP group. To tap the full potential of self-report, more detailed information on pitch-identification strategies and the extent of the AP ability should be assessed in the future. Questions could resemble the following: Is the pitch label immediately available to you without having to apply a cognitive strategy? Is the label verbal, visual, or kinesthetic? Is your AP ability limited to specific pitch classes, timbres, or registers? And what strategies do you use to identify the pitches for which you do not have AP? Underlining the value of self-reported data, Wilson et al. (2009) found that intermediate performers in a pitch-identification task (between 20 and 90 % correct responses) had reported immediate pitch labeling (i.e., what would typically be described as AP) for at least some notes. By continuing to assess such information, it might become clearer if AP is a discrete trait with varying degrees of extent and acuity, or if it is a gradual ability.

By combining detailed self-reports with data from pitch-identification and pitch-production tasks, standardized criteria for AP might ultimately be agreed on. This would greatly increase the comparability between studies and facilitate meta-analyses.

5.4.2 Collaborations and Data Sharing

More specific to neuroscientific AP research is the issue of small sample sizes. Questionnaire surveys and behavioral experiments can be run online, whereas cognitive neuroscience studies depend on the participants to come to the laboratory. This is costly both in terms of time and finances. Additionally, the participants must be willing to travel to the research site, which limits the geographical reach of recruiting. Combined with the relative rarity of AP, this often results in small-sampled studies.

Collaborative and open science can help overcome this inherent limitation to ensure more robust results. By making the materials and the data of published research available online, re-analysis and direct replication studies become possible. More and more publishers acknowledge the importance of data sharing and mandate at least a statement on data availability in research articles. To do our bit, we uploaded the data and materials of article 2 and article 3 of this thesis to a data repository (Open Science Framework: https://osf.io/). Data sharing might be particularly interesting for resting-state data, since they are often routinely acquired before any experiment. If, additionally, multiple research groups from different sites were to collaboratively plan and conduct studies, larger data sets could be acquired in a shorter amount of time. Given that even simple experimental conditions like attentive listening have yielded inconsistent results with regard to the effect of AP, collaborations should first focus on basic experiments.

If and when there finally exist standardized criteria for AP, and the studies are sufficiently powered, we will be one step closer to reveal the neural mechanisms underlying AP.

5.5 Concluding Remarks

The research presented in this thesis contributes to a better understanding of AP and provides valuable insights into the current state of AP research. The results from the two experimental tasks show that both AP and non-AP musicians can detect small changes of 25 cents in tone frequency. Our evidence further suggests that AP musicians can suppress pitch labeling depending on the specific task context. The strikingly similar ERP responses in experimental conditions that do not require pitch identification also indicate that AP

processes in general might not be as automatically triggered as is often assumed. This could explain why the brain networks underlying AP seem to be difficult to measure during resting state. Nonetheless, our resting-state data provided weak evidence that sensory and higher-order brain areas in the perisylvian area are more strongly connected in AP musicians than in non-AP musicians. If replicated, this finding would indicate that both perceptual processes and cognitive functions support the ability of AP. More generally, our studies have demonstrated the need for larger sample sizes and replications in the field. Fostering more robust and replicable research will ultimately lead to better answers to the question of the neural bases of AP.

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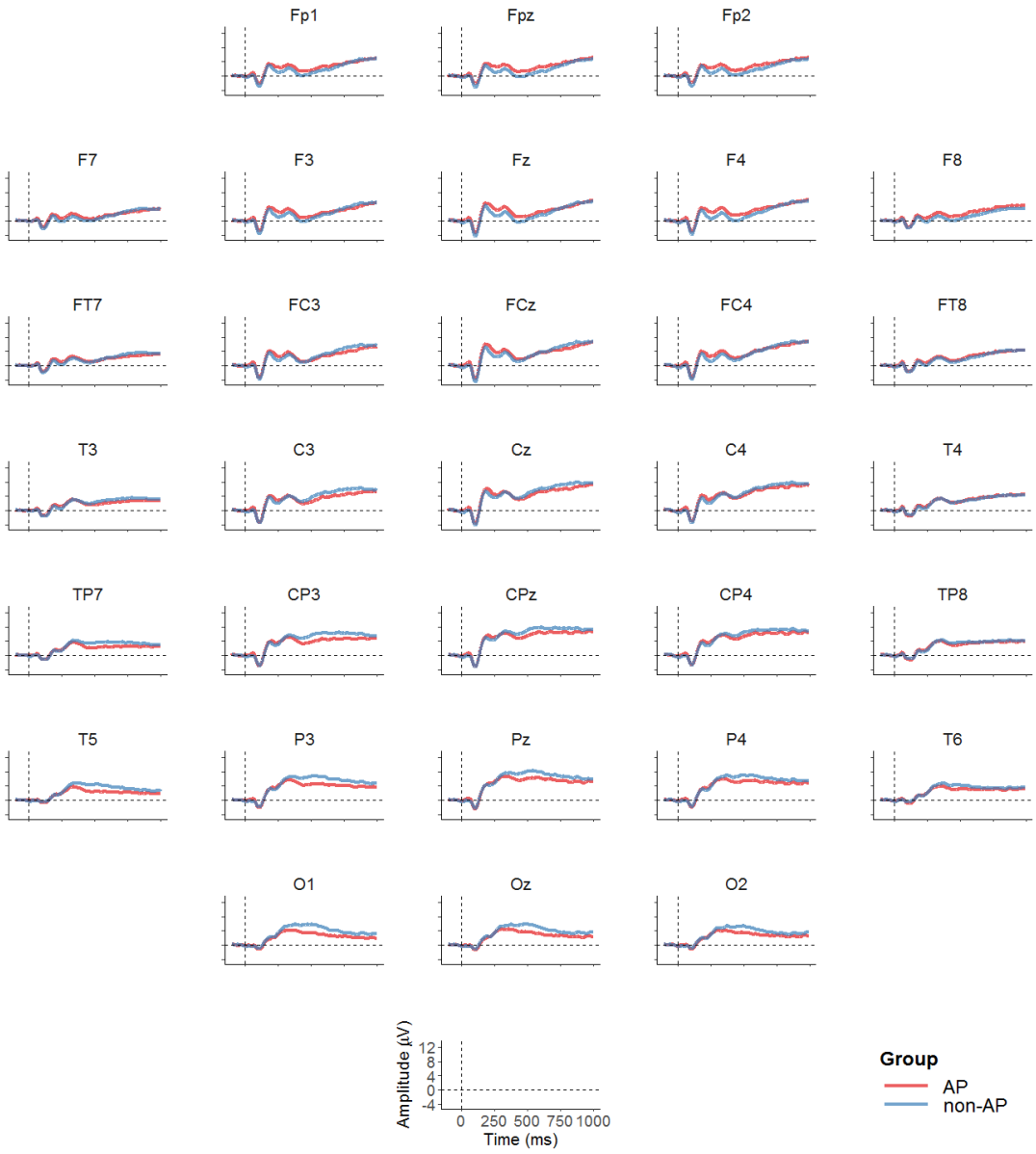
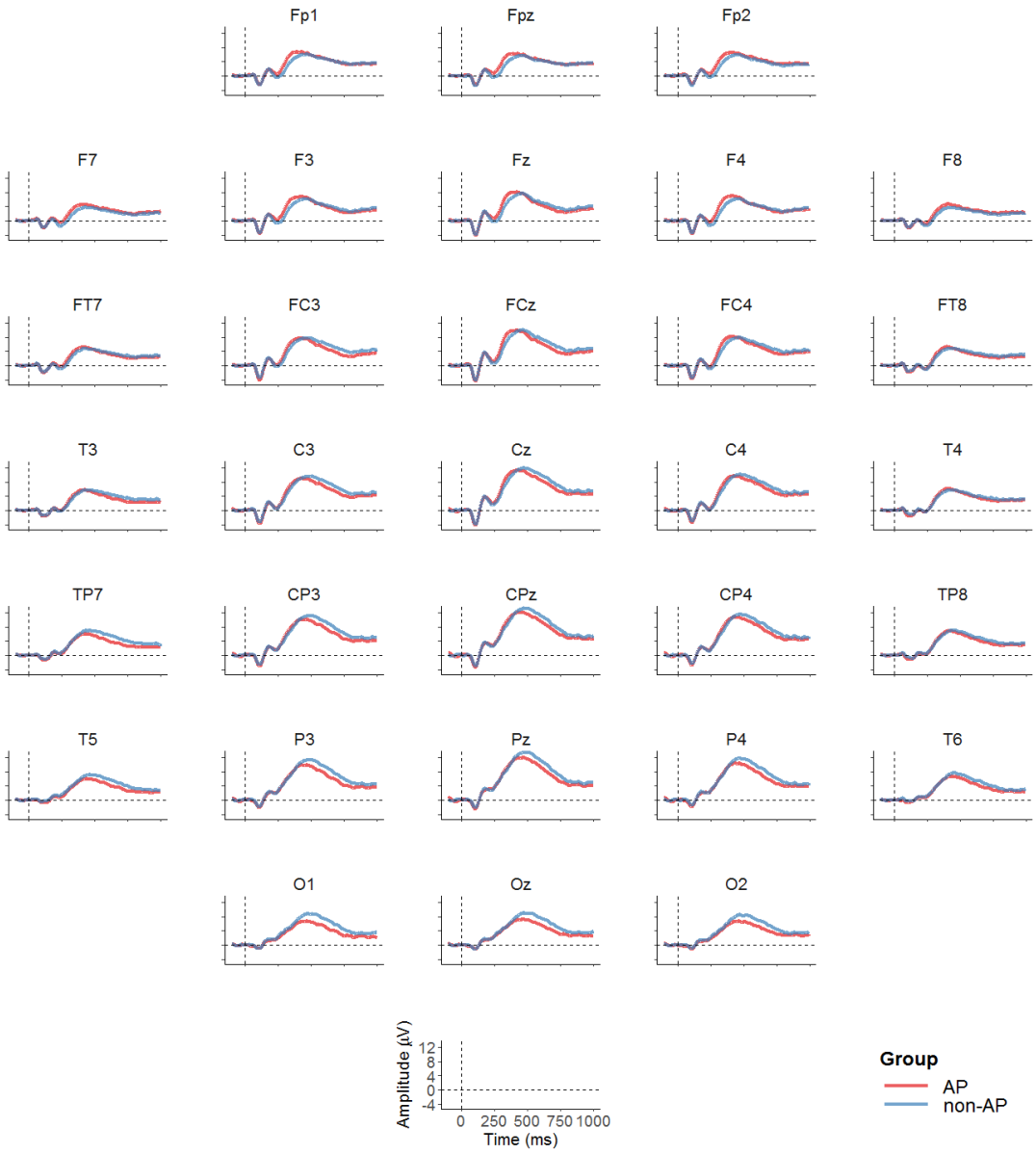
Supplementary Material

Supplementary Figure 1 (Article 3). Grand averages of the event-related potentials (ERPs) over all participants for the three cued conditions in the auditory Go/Nogo task (Go in green, $Nogo_{it}$ in violet, and $Nogo_{mt}$ in orange). Shown at all 31 electrodes.

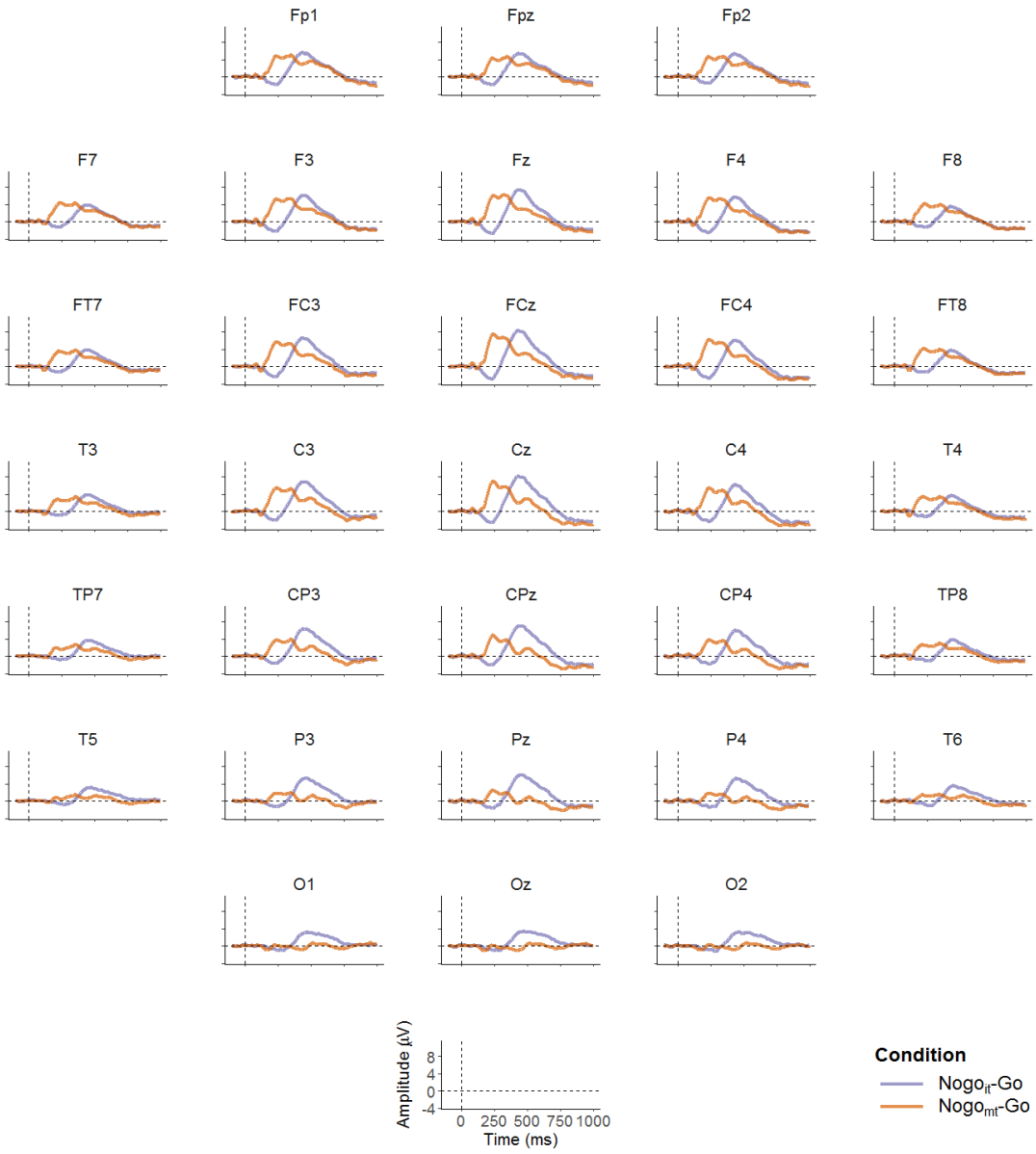


Supplementary Figure 2 (Article 3). Group-averaged ERPs for the Go condition at all 31 electrodes. Musicians with absolute pitch (AP) are shown in red, musicians without AP are shown in blue.

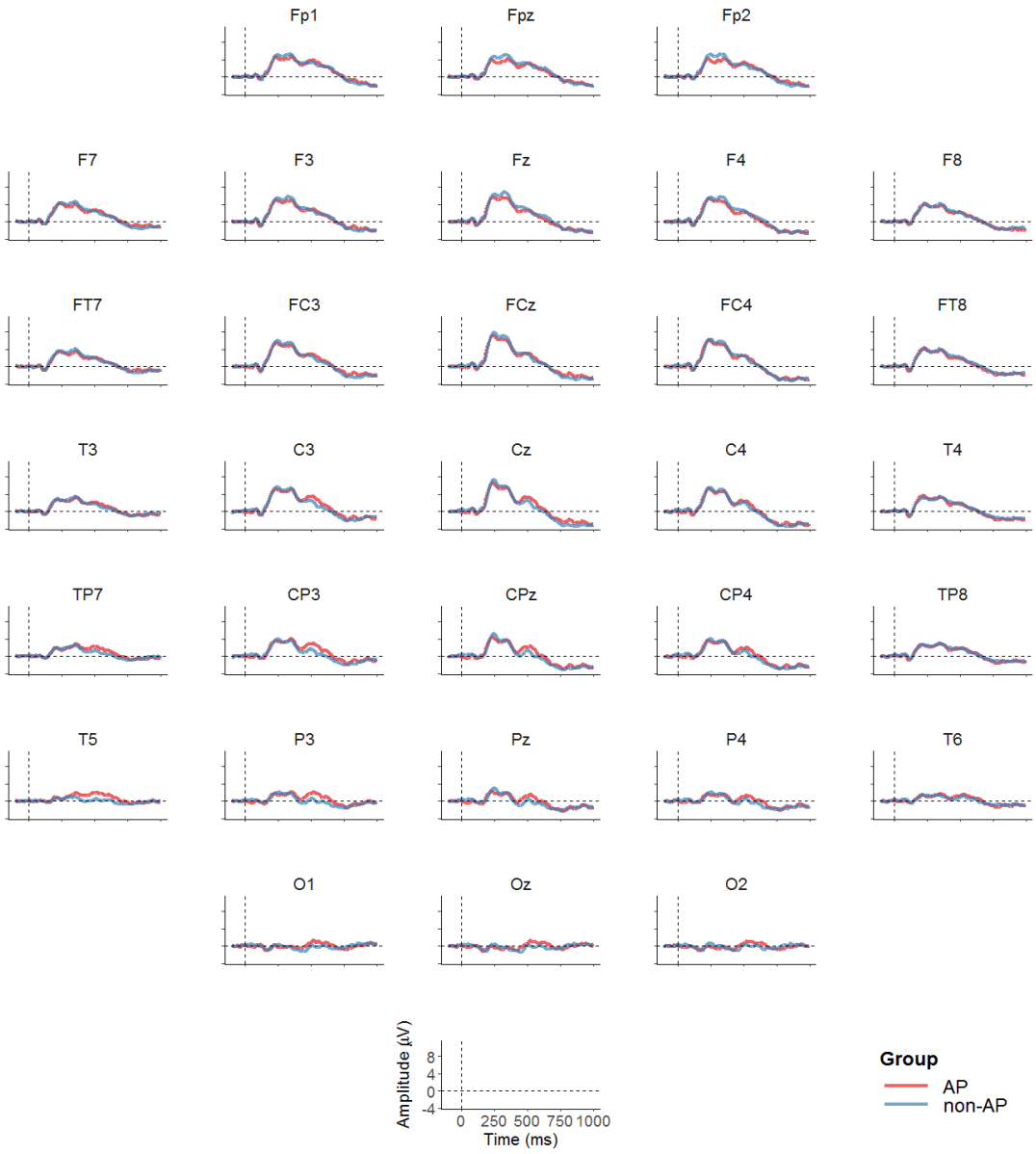
Supplementary Figure 3 (Article 3). Group-averaged ERPs for the $Nogo_{it}$ condition at all 31 electrodes. Musicians with AP are shown in red, musicians without AP are shown in blue.



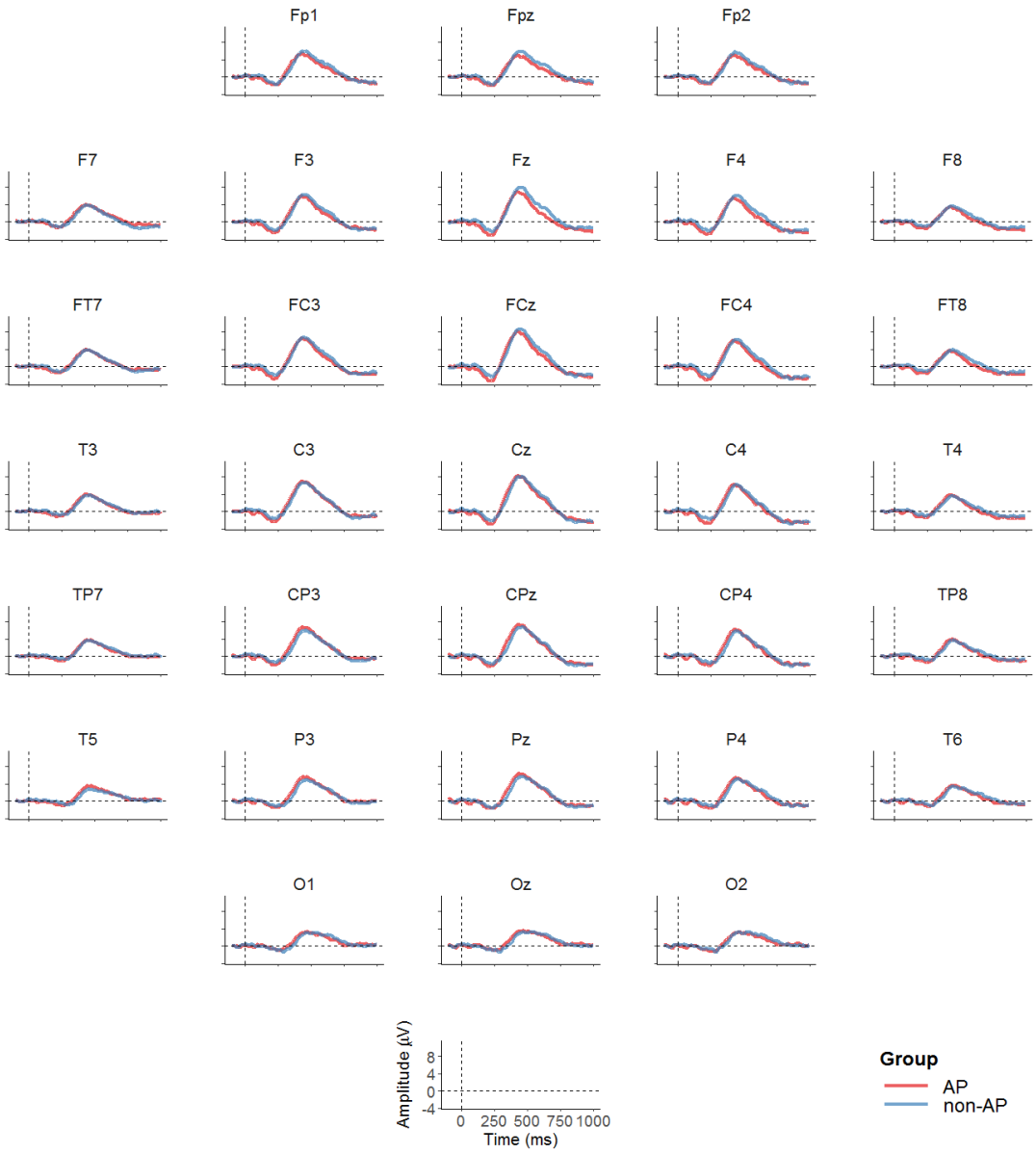
Supplementary Figure 4 (Article 3). Group-averaged ERPs for the $Nogo_{mt}$ condition separately for the two groups at all 31 electrodes. Musicians with AP are shown in red, musicians without AP are shown in blue.



Supplementary Figure 5 (Article 3). Grand averages of the difference waves over all participants at all 31 electrodes. Nogo$_{it}$-Go is depicted in violet, Nogo$_{mt}$-Go is depicted in orange.



Supplementary Figure 6 (Article 3). Group averages of the difference wave $Nogo_{it}$-Go at all 31 electrodes. Musicians with AP are shown in red, musicians without AP are shown in blue.



Supplementary Figure 7 (Article 3). Group averages of the difference wave $Nogo_{mt}$-Go at all 31 electrodes. Musicians with AP are shown in red, musicians without AP are shown in blue.

Curriculum Vitae

Personal Information

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Education

02/2016 – present	**PhD candidate**, University of Zurich Department of Psychology, Division Neuropsychology Advisor: Prof. Dr. Jäncke Co-advisor: Prof. Dr. Frühholz
09/2013 – 01/2016	**Master of Science in Psychology**, University of Zurich Major: Cognitive Psychology and Cognitive Neurosciences Minor: Biology
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Publications

Greber, M., & Jäncke, L. (2020). Suppression of Pitch Labeling: No Evidence for an Impact of Absolute Pitch on Behavioral and Neurophysiological Measures of Cognitive Inhibition in an Auditory Go/Nogo Task. Frontiers in Human Neuroscience, 14, 585505. https://doi.org/10.3389/fnhum.2020.585505

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